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The Biology of *Pandalus montagui* Leach

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INTRODUCTION AND REVIEW OF LITERATURE

THE pink shrimp, *Pandalus montagui* Leach, is fished extensively during the spring and summer months, in the Thames Estuary, from a line south west of Leigh-on-Sea to N. Foreland and Orfordness. In past years it was no uncommon occurrence for pink shrimps to penetrate as far as Thames Haven, approximately 6 miles west of the present line (Fig. 1).

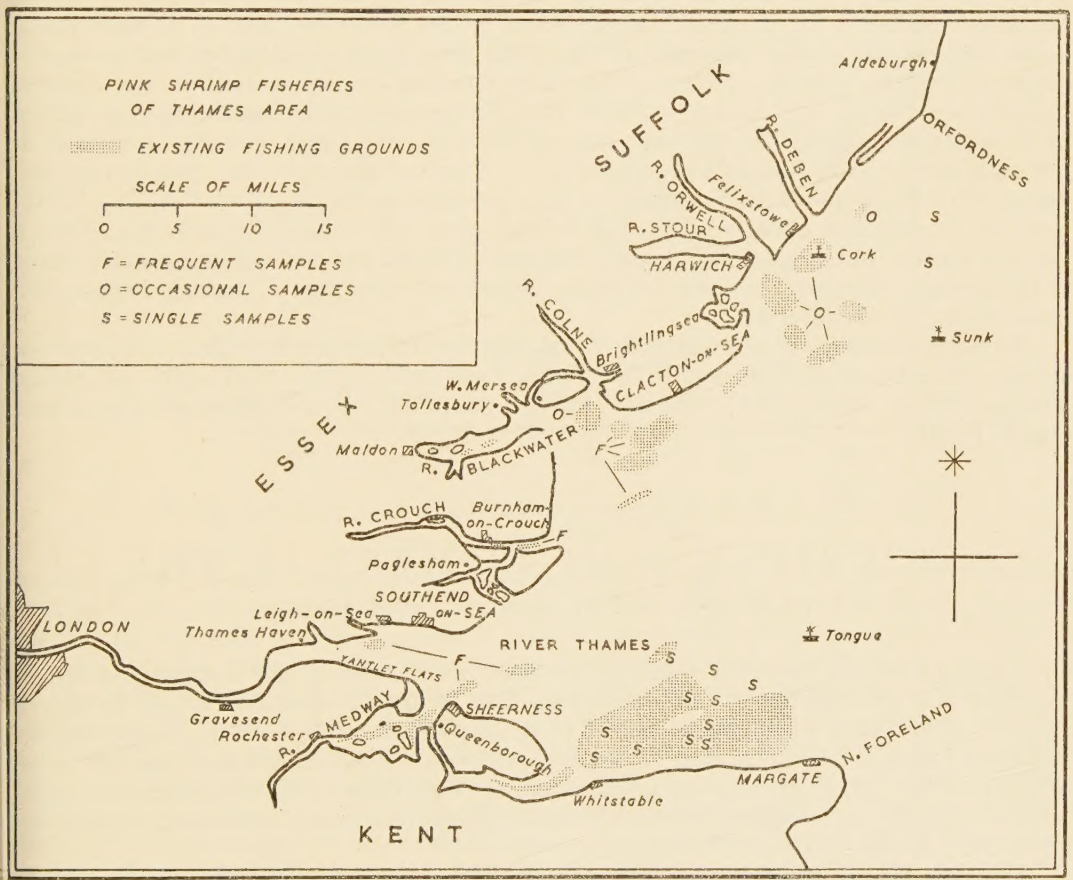


Fig. 1. *Map showing the pink shrimp fishing grounds in the Thames area, and ports where* Pandalus montagui *and* Crangon vulgaris *are landed.*

During the year 1949 the landings of pink shrimps fell considerably, in certain areas by more than 40 per cent. Towards the end of the year 1949 it was decided to investigate the pink shrimp fishery and to study first the biology of the species.

Although *Pandalus montagui* has been recorded from positions extending from the extreme north of Norway to the English Channel, and it has been found in great numbers over the whole North Sea and off parts of north west coast of England, its life history has not been studied in great detail and a controversy arose in 1936 with regard to the occurrence of sex reversal.

Bell (1853) gave a short account of the external morphology of *Pandalus montagui* and records of its occurrence from the British Isles. Calman (1899) was the first author to notice a difference on the endopodite of the first pleopod of three male specimens, which he considered to be due to immaturity. However, he stated that the material at his disposal was not sufficient to elucidate this point. Murie (1903), who was mainly interested in the sea fisheries and fishing industries of the Thames Estuary, included in his report notes on the migratory habits, food, size and breeding season of the pink shrimp. Wollebaek (1908), like Calman, observed 'dimorphism' in the male pink shrimp and believed it to represent a phase of male activity. Wollebaek gave also a short account of the distribution of the species in Norway, the breeding season, size, reproductive organs and secondary sexual characters. Kemp (1910) reviewed the observations of Calman and Wollebaek and added the, by then available, information with regard to its general and local distribution.

The genus *Pandalus* attracted considerable attention at the beginning of the fourth decade of the present century, when Berkeley (1930) demonstrated that four *Pandalus* species (*P. danae*, *P. borealis*, *P. hypsinotus*, *P. platyceros*) and *Pandalopsis dispar* showed the phenomenon of sex reversal. Leopoldseder (1934) presumed that *P. borealis* was a protandric hermaphrodite. Jägersten (1935, 1936) who, like Leopoldseder, had no knowledge of Berkeley's work, arrived at the same conclusions with regard to sex reversal question and growth of *P. borealis*. Jägersten had the opportunity of examining four catches of *P. montagui*, collected on the west coast of Sweden, and stated that this species is in principle similar to *P. borealis* with regard to sex characteristics and their transformations, except that the proportion of primary females is higher in *P. montagui*. Leloup's (1936) work on *P. montagui*, collected from the Belgian coast and southern North Sea, gives a detailed account of the secondary sexual characters and the external and internal structure of the gonads. However, he does not share Jägersten's view that *P. montagui* shows the phenomenon of sex reversal.

Publications mainly concerned with the life history of *Pandalus borealis* or allied species include the following: Hjort and Ruud (1938), Rasmussen (1942, 1945, 1951 and 1953), Tamura (1950), Kubo (1951), Igarashi (1951), Pike (1952), Aoto (1952), and Pruter and Harry (1952).

DESCRIPTION OF FISHERY IN THE THAMES ESTUARY

The pink shrimp is found in variable quantities along most of the English and Welsh coastline, and the methods of catching it vary from district to district. On the Yorkshire coast it occurs only occasionally, mixed with populations of 'brown' shrimp, *Crangon vulgaris* L. In the Severn Estuary brown and pink shrimps are caught in kypes and hose nets (Matthews, 1934). However, catches of pink shrimps from the above mentioned localities are insignificant compared with catches obtained from some other areas, where the beam trawl is used exclusively for fishing.

The total annual landings of shrimps for England and Wales during the past ten years show that they fluctuate between one and a half million and two and a half million kilograms. Unfortunately the official returns of landings do not differentiate between pink and brown shrimps, and it is impossible to deduce the ratio between these two species. However, it is an established fact that pink shrimps are found in considerable densities in the Wash and Thames Estuary, on the east coast, and in Morecambe Bay on the north west coast of England. Landings of pink and brown shrimps at ports on the Wash, Thames Estuary and Morecambe Bay amount approximately to 80% of the total landings (Fig. 2). As far as landings are concerned the Thames Estuary is second in importance, the Wash being first.

The first records of the number of boats and men engaged in the shrimp fishery in the Thames area go as far back as the year 1832, when half a dozen small boats were operating from Leigh-on-Sea (Wells, 1933). The shrimp fishery, however, must have originated much

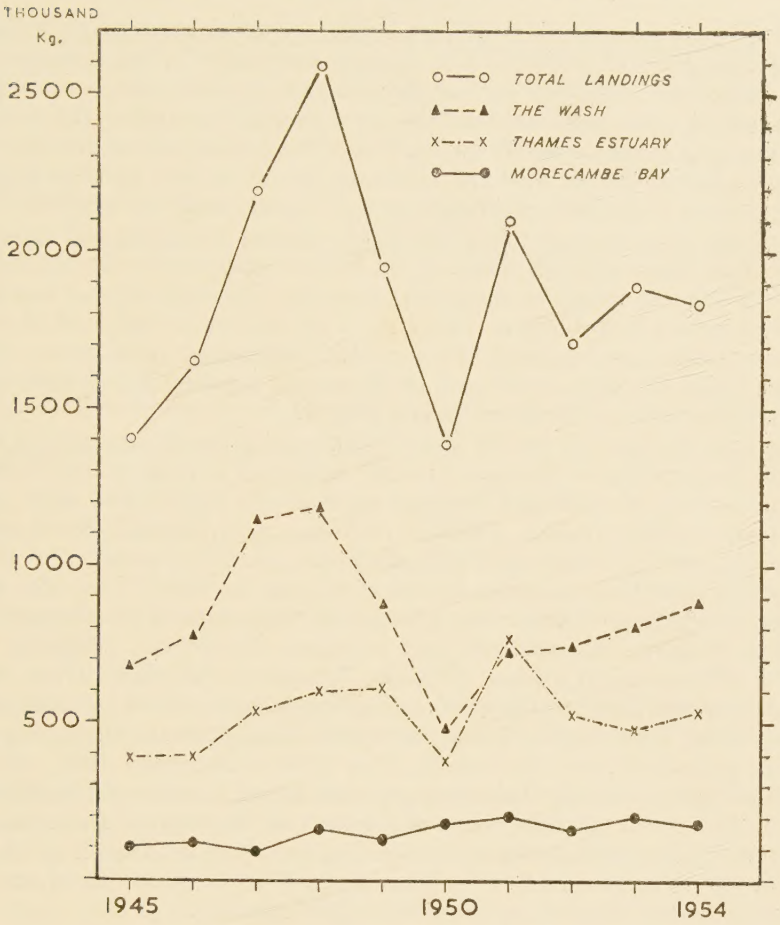


Fig. 2. *Landings of pink and brown shrimps in the three main fishing areas of England and Wales.*

earlier, since it is known that shrimps were sent from Leigh-on-Sea to London by boat or cart until about 1820 (Murie, 1903). According to Murie the first records of Leigh fisheries go back to 13th century, when Henry III granted the right of several fisheries to Hubert du Burgh. With the passage of time more men and boats became engaged from this small town and by 1850 100 boats and 200 people were in the trade. After 10 years the fleet of shrimpers numbered 114 boats, and by 1875 the number rose to about 200, although some of them were engaged in fishing for sprats (*Clupea sprattus*), white-bait (young clupeoids), cockles (*Cardium edule*), winkles (*Littorina littorea*), mussels (*Mytilus edulis*) and oysters (*Ostrea edulis*) in their seasons. After 35 years the numbers of boats dropped to 75. After the World War I, probably owing to the prevailing low prices of shrimps, the shrimping fleet shrank further, the number dropping to 40 boats by 1932, and in 1949 the fleet at Leigh-on-Sea consisted of only 31 boats, with 24 working whole time. In the same year the total number of craft engaged in the shrimp fishery in the Thames area was 110, of which 90 boats were working whole time.

Until the beginning of this century all the shrimp boats were sailing vessels, similar to the Essex sailing smacks and known locally as 'bawleys' (see Plate 1). These bawleys were craft varying from 32 to 42 feet in length and quite a number of them are still in service and have been equipped with engines. There is also a fleet of new boats operating mostly from Leigh-on-Sea. These are square-sterned boats of 30 to 33 feet in length, equipped with diesel engines (see Plates 2 and 3).

The beam trawl is used exclusively for shrimping, the size of beam varying between 18 and 24 feet (see Plate 4(b)). The size of mesh in the cod-end varies between 79 and 94

rows per yard, approximately 19 to 25 mm. mesh, a smaller mesh of 19 to 22 mm. being used when fishing for pink shrimps. The shrimps are cooked at sea in copper boilers (see Plate 5(a)). Before the catch is cooked the shrimps pass through a sieve or riddle (illustrated in Plate 6(a) and (b)), the width between the wires varying from 4·8 to 6·6 mm., so that the small ones may go back to the sea. Seawater is used for boiling and salt added, the quantity depending on whether the shrimps are to be sold locally or sent away to inland markets.

The pink shrimp is distributed throughout the Thames area, but it is found in considerable numbers only on certain grounds, and mainly during the spring and summer months. Occasionally if the weather keeps moderate and water temperatures do not drop considerably, the shoals will stay longer on the fishing grounds. The pink shrimp, in contrast to the brown shrimp, prefers hard bottom. This type of sea bottom is found off Harwich, Felixstowe, Clacton-on-Sea, approaches to rivers Colne, Blackwater and Crouch, south west of Leigh-on-Sea, river Medway, north east of Sheerness, between Whitstable and Margate, and also in certain parts of the river Thames (Fig. 1).

The texture of the bottom on the above mentioned grounds varies from area to area, depending on the presence or absence of certain species of Crustacea and Mollusca, but in most cases it consists of small and medium sized stones with coarse sand and shells of *Mytilus*, *Ostrea*, *Cardium*, *Nucula*, *Chlamys*, *Macoma*, *Abra*, *Spisula*, *Buccinum*, *Ocenebra*, *Gibbula*, *Nucella*, etc. The stones and large shells are usually encrusted with the sedentary polychaete worm *Sabellaria spinulosa* known commonly as 'ross'. They also usually bear different species of algae, coelenterates (*Sertularia*, *Halecium*, *Hydrallmania*), bryozoans (*Membranipora*, *Flustra*, *Alcyonidium*), and ascidians (*Dendrodoa*, *Molgula*). In addition certain species of Crustacea (*Carcinus*, *Portunus*, *Eupagurus*, *Porcellana*, *Hyas*, *Macropodia*), echinoderms (*Asterias*, *Solaster*, *Ophiura*) and of fish (*Agonus*, *Gobius*, *Gadus*, *Pleuronectes*, *Raja*, *Liparis*, *Solea*, *Onos*, *Clupea*, *Cottus*) are quite common on the shrimping grounds.

During the period of thirty-two months, May 1950 to December 1952, when 130 trawl hauls were made on the existing shrimping grounds, a total number of 151 different species was recorded. Additional information on the texture of the bottom and of the fauna was obtained by employing an ordinary oyster dredge, provided with teeth on the blade and lined with canvas or small-meshed shrimp netting. The complete list of the fauna with notes on their frequency is given in Appendices I, II and III.

After 1952, when further trawl hauls were made over the same grounds, species, which had been previously observed once or twice, occurred more frequently and the following eleven additional species were recorded: *Chrysaora isosceles*, *Tealia felina*, *Stylarioides plumosa*, *Gammarellus homari*, *Philine aperta*, *Henricia sanguinolenta*, *Galeus vulgaris*, *Atherina presbyter*, *Raniceps raninus*, *Caranx trachurus* and *Trigla pini*. The English rough tingle (*Ocenebra erinacea*), which previously had been recorded only as dead shells (Appendix II), was found in small numbers on several occasions below Clacton-on-Sea and off Harwich (Mistakidis and Hancock, 1955).

It has been mentioned above that *P. montagui* prefers hard bottom, in contrast to *C. vulgaris*, which prefers soft muddy sand. However, there is no definite demarcation line between pink and brown shrimp populations, and their ratio in the catches varies considerably. Catches of pink shrimp obtained from three different areas, Clacton-on-Sea, river Crouch and river Thames (Fig. 1), were found to contain, especially during the winter and spring months, a high percentage of brown shrimps. On several occasions the percentage of brown shrimp was as high as 80% to 93% (Fig. 3). Catches with such high percentages can be accounted for by the fact that they were obtained from grounds which are in the proximity of muddy sand bottom. It is not uncommon for a shrimp boat to trawl for a short period on both pink and brown shrimp grounds, especially if there is a strong tide and wind. In addition pink shrimps are relatively scarce during the winter months, and the brown shrimp becomes the dominant species.

The average percentage of brown shrimp in the catches varies usually between 2% and 20%. The mean percentages of brown shrimp in the catches obtained from grounds off Clacton-on-Sea, in the river Crouch and in the river Thames, over a period of 25 months, were respectively 16·27%, 29·56% and 34·80%. If the catches obtained during the winter months are omitted then the percentage of brown shrimps will be considerably smaller.

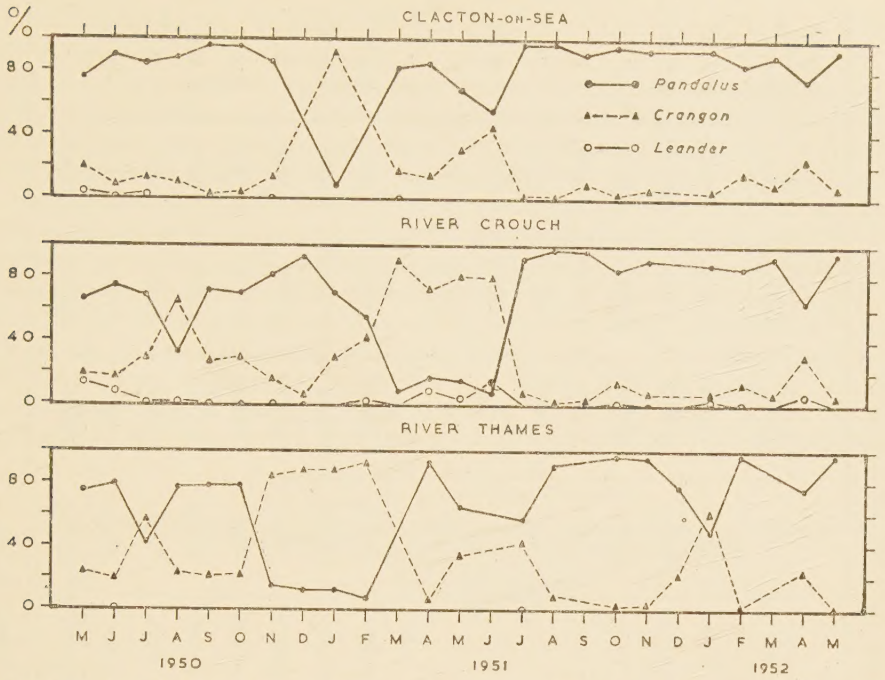


Fig. 3. *Percentages of* Pandalus montagui, Crangon vulgaris *and* Leander spp. *appearing in catches obtained from grounds off Clacton-on-Sea, and in rivers Crouch and Thames.*

A small percentage of prawns, *Leander serratus* and *Leander squilla* appeared in the catches, most frequently from the grounds in the river Crouch (Fig. 3).

The brown shrimp (*C. vulgaris*) is fished only in small numbers on the north side of the Thames Estuary, and it follows that shrimp boats operating from Tollesbury, West Mersea and Brightlingsea (Fig. 1) concentrate only on the pink shrimp fishery. When the shoals of pink shrimps have disappeared from the nearby fishing grounds, the Tollesbury and Brightlingsea boats either are laid up for the winter, or convert their gear for the sprat fishery which begins in late October or early November. In contrast, fishermen from Leigh-on-Sea, Rochester and Queenborough can turn, without difficulty, to the brown shrimp which is found all the year round on the south bank of the river Thames, from Yantlet Flats to Sheerness and further east.

The average catch of pink shrimps during one hours' trawling is about 7 to 15 gallons (32 to 68 litres), the quantity depending on the fishing grounds and season of the year. Catches of 50 to 60 gallons are not unusual and during the summer of 1952 certain boats from Southend-on-Sea secured hauls of 80 to 100 gallons of pink shrimps per hour.

The abundance of *P. montagui* fluctuates from year to year. During the summer of 1950 trawling on grounds extending from Clacton-on-Sea to Sheerness did not yield more than 3 gallons per hour. Similar small catches were observed during the previous summer in the Wash. This unusual disappearance of pink shrimps from the existing fishing grounds, for which an explanation is offered below, resulted in a sharp decline of landings in the Wash and the Thames areas (Fig. 2). In the Thames area, where a substantial quantity of brown shrimps was landed during 1949 and fishing boats from Whitstable and Margate were successful in securing catches of pink shrimps, the decline was less apparent (Table I).

During the year 1951 pink shrimps became more abundant in the Wash and the Thames area, and the landings increased. However, whereas the landings in the Wash remained at the same level for the next two years, landings in the Thames area showed another decline (Fig. 2). It is not unlikely that the above decline of landings during 1952 and 1953 could be attributed to the demand for 'white weed' (*Sertularia argentea*). Returns from sales of *Sertularia* were exceptionally good, and a certain number of shrimp boats concentrated their efforts on fishing this hydroid.

Table I: Landings of shrimps in the Thames Estuary during the years 1945 *to* 1954

Port	*Year*										*Type of shrimp fished*
	1945	1946	1947	1948	1949	1950	1951	1952	1953	1954	
Felixstowe Ferry . .	–	6603	10819	23669	22603	8634	17473	18844	23416	19860	P & B
Harwich	17269	35098	41701	44952	31441	21384	40228	41803	39060	58463	P & B
Brightlingsea . . .	12292	36317	103212	118247	52012	7974	117181	65016	61612	61460	P
West Mersea . . .	7669	10615	32609	27225	9244	–	101	2082	1067	5435	P
Tollesbury . . .	–	–	–	–	–	–	–	1219	1879	3454	P
Maldon	–	–	–	761	2438	–	–	–	2590	1524	P & B
Burnham-on-Crouch . .	–	–	–	–	–	–	–	1067	1371	457	P
Paglesham . . .	–	–	–	–	50	50	–	–	–	–	P
Southend-on-Sea . .	37993	52266	68419	67098	95339	35707	80812	18946	19606	19606	P & B
Leigh-on-Sea . . .	217752	202971	212825	217244	228825	186006	342958	215111	200838	177270	P & B
Gravesend . . .	86146	46780	41650	43174	23009	22603	26057	19200	27378	21536	B
Rochester . . .	–	–	–	–	51758	49676	90717	76546	69232	71314	P & B
Queenborough . . .	8330	7111	23263	28038	15898	16152	21028	11682	7670	6400	P & B
Whitstable . . .	–	–	–	23060	43123	5384	6044	28292	12597	62527	P
Margate	–	–	–	4165	34082	25600	27885	26260	17524	24178	P & B
Total Kgs. . . .	387451	397761	534498	597633	609822	379170	770484	526068	485840	533484	

P = Pink (*Pandalus montagui*). B = Brown (*Crangon vulgaris*).

METHODS AND SOURCE OF MATERIAL

WHENEVER possible samples of *Pandalus montagui* were collected at monthly intervals, from May 1950 to May 1951, either from commercial catches, taken from the Thames and Clacton-on-Sea grounds, before the shrimps were sorted and cooked, or from catches made by a 6 foot beam trawl fished in the river Crouch. In early 1952, this net was replaced by a 12 foot beam trawl, operated from a 30 foot motor vessel. Sampling was continued for another 18 months, attention being paid to the distribution and abundance of *P. montagui*, and the type of sea bottom. The 6 foot shrimp trawl had a full mesh of 19 to 20 mm. (from knot to knot) in the cod-end, while the commercial nets had a full mesh of 19 to 22 mm. in the cod-end. The aim was to secure 600 to 800 specimens from which 400 were measured and at least one third of the measured sample was sexed. During the winter months of 1950-51 pink shrimps were relatively scarce and it proved difficult to obtain large samples. Occasionally the ratio of brown to pink shrimps, especially from catches in the river Thames, was so high (Fig. 3) that *Pandalus* were picked out from the total catch and from

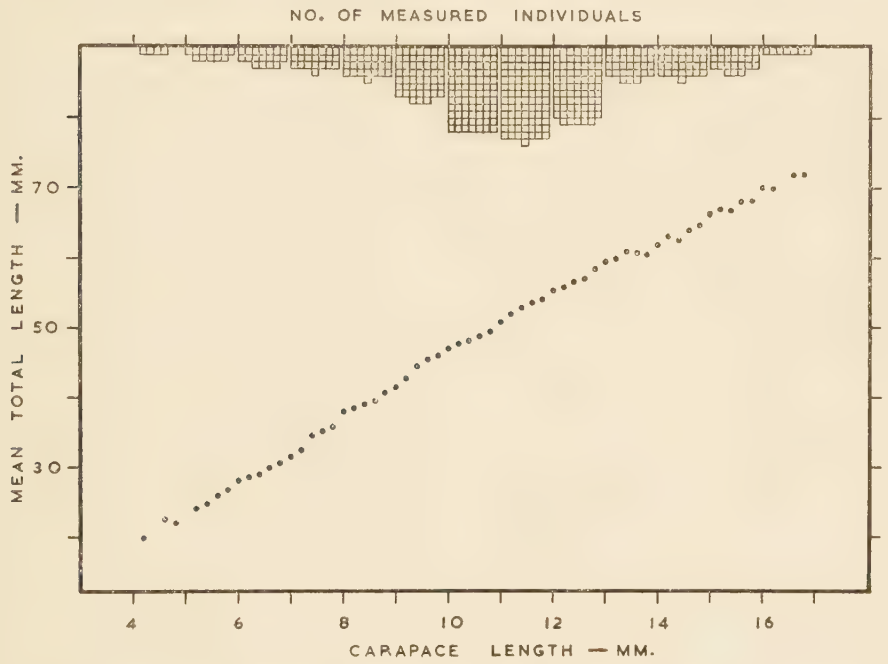


Fig. 4. *Relationship between carapace and total length in* Pandalus montagui.

those gathered a random sample was obtained. In all, up to the end of 1952, about 25,000 specimens had been measured and about 15,000 sexed.

Specimens which were to be measured and sexed were placed without delay into 4 to 5% formalin, and those for histological examination into Heidenhain's Susa. Bouin's picro-formol fixative did not prove to be satisfactory when gonads of *Pandalus* were to be sectioned. Cross sections of gonads were cut at a thickness of 8-10 μ and stained in Ehrlich's Acid Haematoxylin and Eosin.

The measurement of all specimens was based on the carapace length, the distance from the base of the eye notch to the posterior mid-dorsal edge of the carapace. This method has advantages over the measurement of the total length, from the tip of the rostrum to the posterior edge of the telson, as in many preserved samples the rostrum is damaged and the abdomen flexed. Leloup (1936) measured his samples from the tip of the antennular scale to the posterior edge of the telson. In the present case an ordinary screw-micrometer fitted with special jaws (Cole and Mistakidis, 1953) was used and shrimps were measured to 0·2 mm. The data were subsequently aggregated into 1·0 mm. groups.

The relationship between carapace length and total length (from the tip of the antennular scale to the posterior edge of the telson) is shown in Fig. 4. The ratio of total length to carapace length, based on the measurement of 480 specimens, ranged from 4·76 to 4·28, becoming smaller with increase in the total length. The mean ratios for specimens less and over 10·0 mm. carapace length were respectively 4·64 and 4·47. By multiplying the carapace length by 4·5, which is the approximate mean ratio of all measurements, one can obtain the approximate total length of the pink shrimp.

Fig. 4 does not include two large pink shrimps, fished in 1954 and 1955, measuring 18·2 and 19·0 mm. carapace length respectively, with total lengths of 77 and 80 mm.

BREEDING

No information was available on the breeding season of the pink shrimp, prior to the beginning of this century. Sars (1900), who described the development of the post-embryonic stages of *P. montagui* from the Norwegian coast, did not mention its breeding season. Murie (1903) was the first author to confirm previous private observations that the pink shrimp on the south east coast of England has only one spawning season, commencing about November and terminating in May. Wollebaek (1908) observed berried females of *P. montagui* in the Norwegian fjords from the last days of November until the first days of June. He added that the "breeding time of this species appears to be identical with that of *Pandalus borealis*". Wollebaek (1903), however, had found ovigerous females of *P. borealis* in the early part of September. Rasmussen (1951, 1953), states that spawning of *P. borealis* in the Arctic waters of Spitsbergen takes place three months earlier than in southern Norway, and the eggs hatch two months later during the following spring. He also remarks that "the colder the environment, the earlier the spawning and the longer the ovigerous period". Jägersten (1936) found five specimens carrying relatively freshly laid eggs, from a catch obtained in the Gullmar Fjord, west coast of Sweden, on July 18, 1935. Leloup (1936), who collected specimens of *P. montagui* from the southern part of the North Sea, states that ovigerous females are present during the winter and spring months, chiefly from February to May. None of the above authors has supplied any information on when the first signs of ovarian maturity appear, or the percentage of ovigerous females, or the number of eggs carried by female shrimps. Murie (1903) stated, however, that the number of eggs in *P. montagui* is fewer than in *Crangon vulgaris*.

The ovaries of the pink shrimp in the Thames area begin to mature in August, sometimes in July, when the posterior part of the gonad assumes a pinkish-yellow colour. Gradually the gonad expands and begins to cover the posterior part of the stomach, eventually enveloping the stomach and expanding laterally on both sides of the carapace. The colour becomes greenish-blue towards the end of October. The different stages of maturity are shown in Table II.

It will be seen from Table II that the majority of the females, during the winter of 1951-52, reached the mature stage in November. A small number of females reached this stage in October, and a small percentage possessed mature ovaries as late as March and April. It is probable that these individuals would have spawned in April or May. During the winter of 1952-53 observations on samples from the river Crouch showed that the majority of the female population reached the mature stage in December.

Observations of this kind were not made during the year 1950-51, but it is most likely that the breeding pattern followed similar lines. Records of females with developing ovaries, trawled on the same grounds during 1950-51, showed that the peak was reached in November, except for females from the river Crouch where the peak was reached in December (Fig. 5). No figures are given after January 1951, as the number of female shrimps in the samples was very small, and the picture would have been misleading.

Egg laying commences at the beginning of November, approximately 10 to 12 weeks after the first signs of ovarian maturity, and continues until January or February (Fig. 5). A small percentage will spawn even later than March, judging from their gonads which become

Table II: Development of ovaries in female P. montagui *during* 1951-52 *in R. Crouch, Clacton-on-Sea and R. Thames*

River Crouch					*Clacton-on-Sea*					*River Thames*				
Date	*Percent. of Maturity*				*Date*	*Percent. of Maturity*				*Date*	*Percent. of Maturity*			
	25 *Nos.*	50 *Nos.*	75 *Nos.*	100 *Nos.*		25 *Nos.*	50 *Nos.*	75 *Nos.*	100 *Nos.*		25 *Nos.*	50 *Nos.*	75 *Nos.*	100 *Nos.*
27 Aug. 51	4	–	–	–	24 Aug. 51	2	–	–	–	8 Aug. 51	5	–	–	–
26 Sept. 51	–	9	–	–	27 Sept. 51	3	–	–	–	–				
26 Oct. 51	8	12	7	8	26 Oct. 51	12	19	3	12	9 Oct. 51	12	20	10	2
26 Nov. 51	1	8	9	129	23 Nov. 51	1	5	10	30	7 Nov. 51	–	55	33	121
–					–					4 Dec. 51	–	–	3	39
3 Jan. 52	–	3	1	20	7 Jan. 52	–	–	–	2	21 Jan. 52	–	–	–	1
5 Feb. 52	–	3	1	5	5 Feb. 52	–	–	–	–	20 Feb. 52	–	–	–	–
4 Mar. 52	–	–	–	1	6 Mar. 52	–	–	–	1	–				
21 Apr. 52	–	–	–	2	4 Apr. 52	–	–	–	–	3 Apr. 52	–	–	–	–
28 May 52	–	–	–	–	5 May 52	–	–	–	–	16 May 52	–	–	–	–
–														
–														
27 Aug. 52	–	–	–	–										
26 Sept. 52	16	1	–	–										
30 Oct. 52	5	39	16	34										
28 Nov. 52	–	8	7	51										
22 Dec. 52	4	21	22	141										

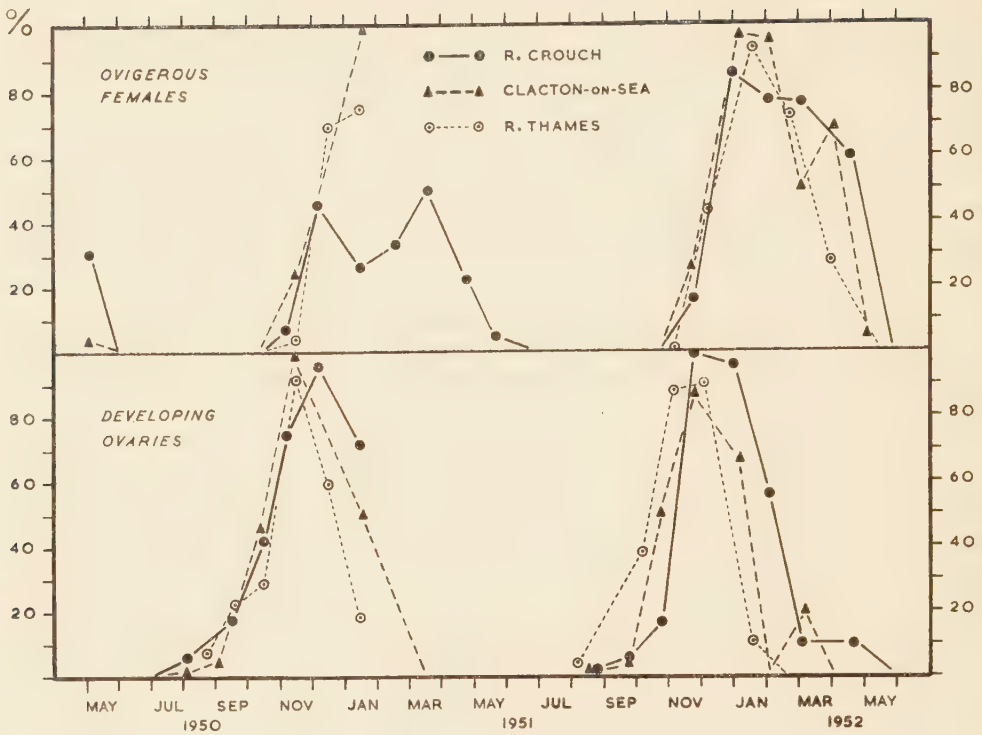


Fig. 5. *The breeding season of* Pandalus montagui.

mature in March or April (Table II). It is quite probable that spawning commences in certain years as early as the middle of October, since a small number of ovigerous females was found in a sample trawled near the Cork Light Ship, about 2 miles south east of Felixstowe (Fig. 1), on 23 October, 1951, and also in a sample from the river Crouch on 30 October, 1952.

The eggs are retained in the egg chamber by the assistance of the ovigerous setae, which secrete a transparent cement-like substance. These setae develop before oviposition, but after the enlargement of the epimera. On several occasions ovigerous setae were observed to be fully developed as early as the second week of October.

The larger size groups of *P. montagui* lay first, followed by the females which will spawn for the first time in their life (Fig. 6). Individuals of carapace length of 13 mm. and over are considered to be of two to three years of age. In the samples from the Clacton-on-Sea area and the river Crouch, one can observe some female individuals which have spawned before completing a full year, since they are of only 10 to 12 mm. carapace length. However, the above two samples were collected at least a fortnight after the sample from the river Thames, in which no young ovigerous females were to be found. Similar results were obtained during the winter of 1950-51, for the three stations, and for the river Crouch during the winter of 1952-53. It was of interest to observe that no young ovigerous females were found during the first month of spawning in the winter of 1950-51.

By the end of January or the beginning of February the majority of the female population has spawned (Figs. 5 and 6). During a period of six years, 1950-55, no ovigerous females were observed after the end of May and this confirms Murie's (1903) statement that the spawning season in the pink shrimp terminates by May. It may be possible, however, to find a very small number of ovigerous females in June, since some of them possess mature ovaries as late as April, (Table II). Mr. V. Foreman, a shrimper from Whitstable, has observed occasional ovigerous females in June.*

The eggs when first laid are emerald green. With the gradual development of the egg the emerald green colour disappears and becomes light green with a tint of light violet.

*A small number of ovigerous females was found in samples trawled in the R. Crouch, during the first week of June, 1956.

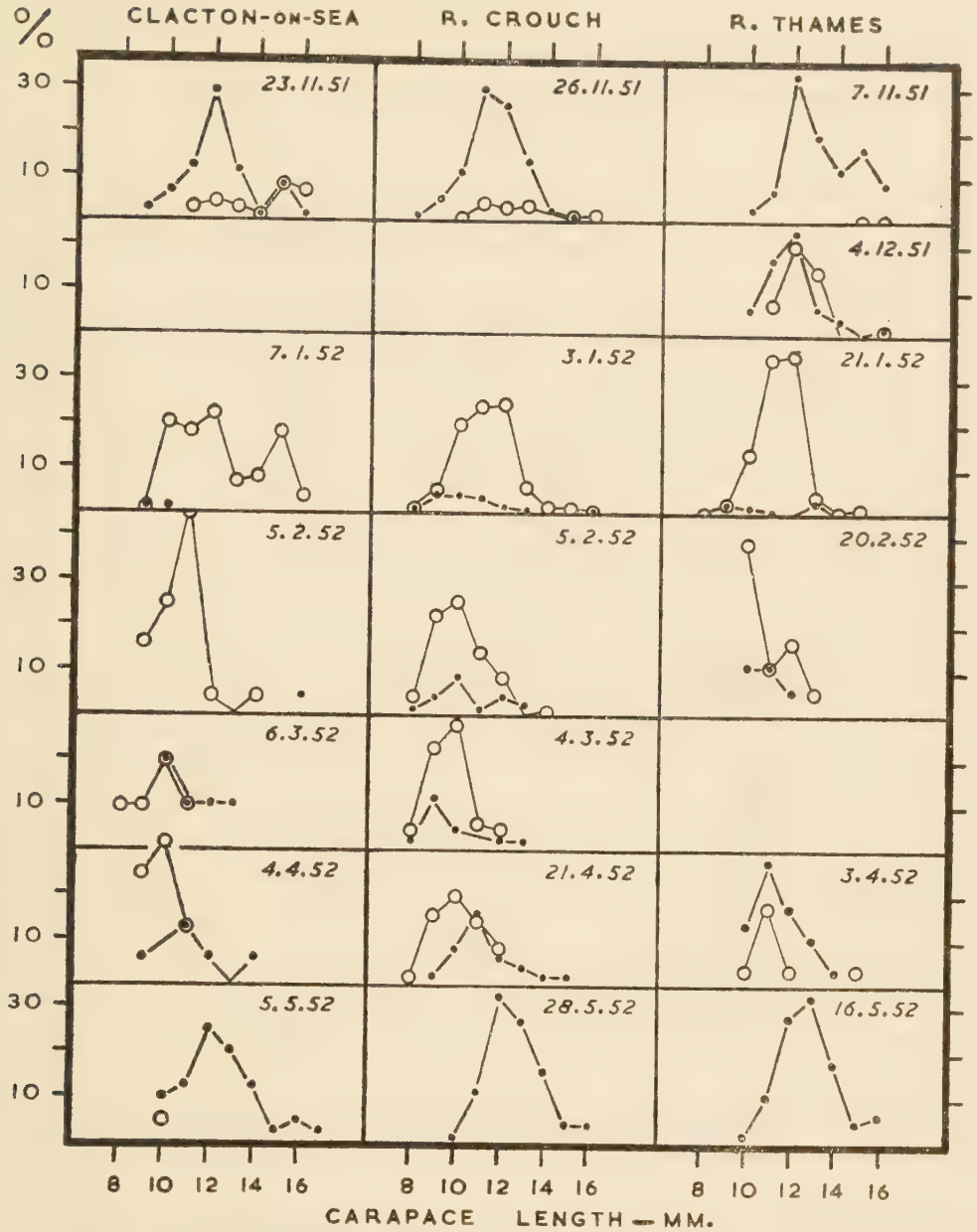


Fig. 6. *Size distribution of breeding and non-breeding females of* Pandalus montagui.
●—● *Neuter or with developing ovaries.* ○—○ *Ovigerous females.*

When the eggs are laid in November they measure approximately 0·78 by 0·60 mm. The measurement of the long axis of 3,050 eggs, comprising 50 eggs taken at random from the smallest to the largest ovigerous females in the samples examined, showed that there was no direct correlation between egg size and carapace size of the parent. If there was any difference in size, it was mainly due to the advanced stage of development in the egg.

During the first three months of incubation the eggs showed no substantial increase in size, although a small increase was apparent during January (Fig. 7). By February many eggs were still 0·80 mm. in length, although a considerable percentage showed an increase in size, mainly those exhibiting late gastrula and 'early' eye-pigmentation stage. With the assumption that some of the eggs were laid as late as January or February (p. 8) the absence of development during February is understandable. With the passage of time the

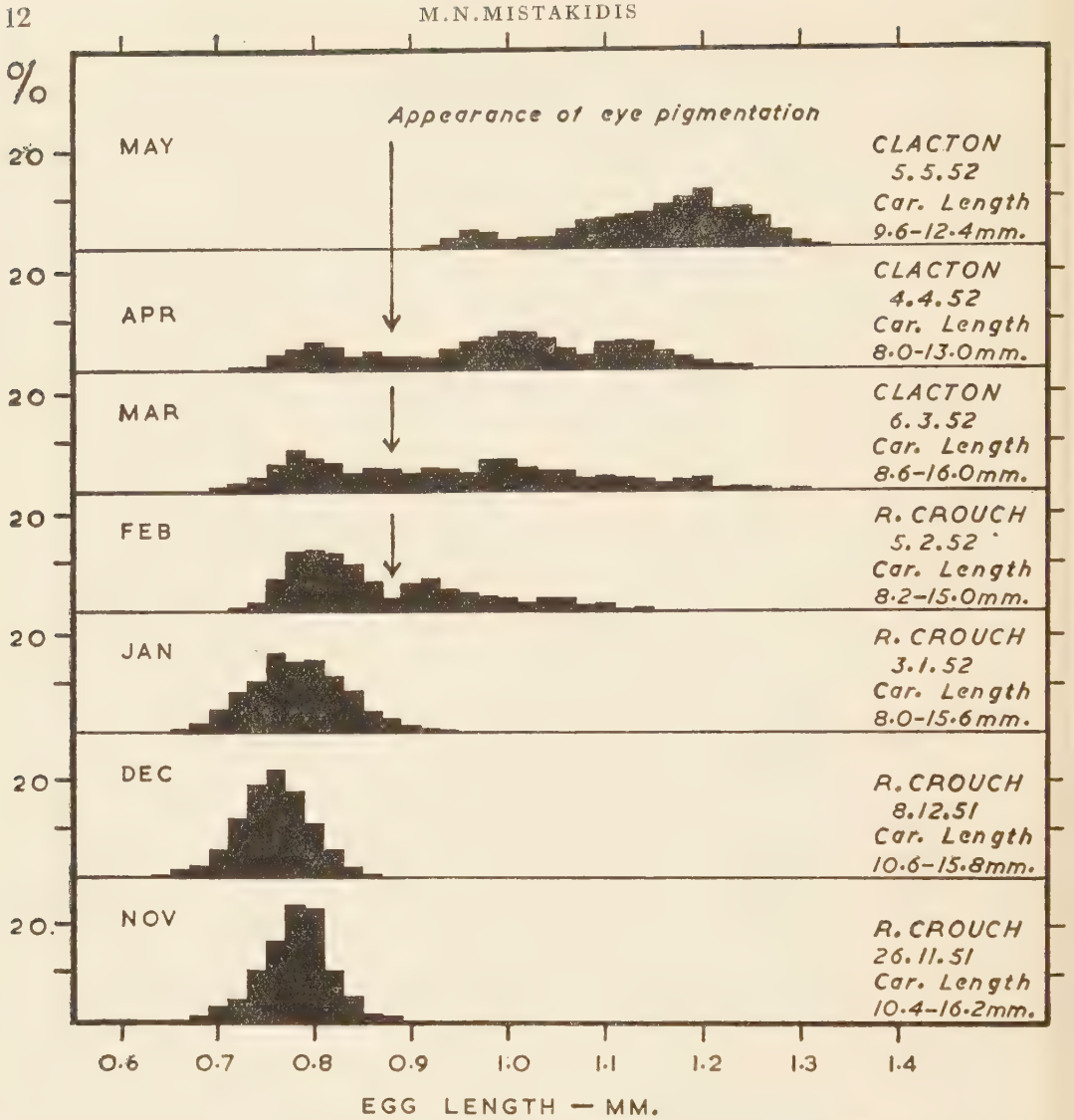


Fig. 7. *Histograms showing the development and appearance of eye-pigmentation, in eggs of* Pandalus montagui. *The first recorded appearance of eye-pigmentation occurred in January* 1952 (*Table III*), *but this sample is not included above.*

size increased and the development of the egg reached the final stage. By April and May the majority measured between 1·00 and 1·20 mm. in length, all being in 'early' or 'late' eye-pigmentation stage. Generally 'early' eye-pigmentation appeared above 0·88 to 0·90 egg-length, and 'late' eye-pigmentation above 0·98 mm. Those eggs which by April were still about 0·80 to 0·90 mm. were in late blastula or gastrula stage.

The examination of 1,800 ovigerous females during the breeding season of 1951-52 showed that the first signs of the embryo showing eye-pigmentation appeared during January, approximately two months after the first oviposition. At this stage the eye-pigmentation can be distinguished only through a microscope, in contrast to the 'late' eye-pigmentation, which can be observed with the naked eye. In the 'late' eye-pigmentation stage the eyes of the embryo measured 0·12 to 0·20 mm., and the yolk did not occupy more than 1/5 to 1/4 of the volume of the egg.

Hatching must take place shortly after the 'late' eye-pigmentation stage is reached, and it is probable that the first larvae are liberated by the end of February or the beginning of March. An ovigerous female with partly hatched embryos was observed as early as

Table III: Appearance of eye-pigmentation in P. montagui *eggs during* 1951-52

Date	*Locality*	*Ovigerous* ♀♀ *Nos.*	*% Early Eye-pigmentation*	*% Late Eye-pigmentation*	*% Total eyed*	*Depth in Metres*	*Temperature °C.*	
							Surface	*Bottom*
7 Nov. 51	R. Thames	2	–	–	.	12·8–13·6	10·45–10·15	10·20–10·20
23 Nov. 51	Clacton	85	–	–	–	11·0– 8·0	9·30– 8·85	9·20– 8·90
26 Nov. 51	R. Crouch	28	–	–	–	7·3– 5·5	8·80– 8·60	–
4 Dec. 51	R. Thames	36	–	–	–	11·0– 5·5	7·75– 7·75	7·70– 7·80
3 Jan. 52	R. Crouch	145	–	–	–	9·5– 7·5	4·50– 4·55	4·70– 4·70
7 Jan. 52	Clacton	370	0·81	–	0·81	11·3–12·0	5·65– 5·60	5·50– 5·50
21 Jan. 52	R. Thames	540	4·62	–	4·62	6·0– 7·3	4·00	4·10
5 Feb. 52	R. Crouch	54	1·85	–	1·85	9·0–10·0	1·60	1·40
5 Feb. 52	Clacton	160	6·87	1·87	8·74	11·5–14·0	2·05– 2·50	2·35– 2·55
20 Feb. 52	R. Thames	40	12·50	2·50	15·00	4·6– 6·0	3·30	3·20
4 Mar. 52	R. Crouch	33	3·03	3·03	6·06	9·0– 5·5	4·75	4·60
6 Mar. 52	Clacton	36	16·66	2·77	19·43	8·0–13·0	4·85– 4·80	4·55– 4·45
3 Apr. 52	R. Thames	23	26·08	56·52	82·60	14·6–13·7	4·90– 5·20	4·85– 4·80
4 Apr. 52	Clacton	95	16·84	44·21	61·05	10·0–12·8	5·00– 5·05	4·70– 4·70
21 Apr. 52	R. Crouch	30	20·00	70·00	90·00	12·8– 5·5	12·00	11·90
5 May 52	Clacton	8	–	100·00	100·00	12·8–11·0	11·75	11·40
16 May 52	R. Thames	–	–	–	–	7·3– 9·0	14·30	14·10
28 May 52	R. Crouch	–	–	–	–	12·8– 7·3	16·90	16·85

28 February 1951, and two cemented females were found in a sample trawled off Clacton on 6 March 1952. A few females possessing ovigerous setae, but without developed ovaries, the eggs of which must have hatched earlier, were observed in a sample from the river Crouch on 4 March 1952. A small number of cemented females was observed in samples taken off the north Wales coast. Three cemented females were found in samples taken between Puffin Island and Ormes Head, 3 March 1953, and four in Puffin Hole on 23 March 1953.

Since the percentage of advanced embryos is comparatively small during February and March, the number of hatched larvae must also be small (Table III). Liberations on a large scale must occur during April, as the percentage of ovigerous females after April, during 1951 and 1952, was less than 10% (Fig. 5). Observations of ovigerous females kept in the laboratory showed that 75% had hatched between 9 and 28 April 1954. The hatching period may vary from year to year, and also from area to area. Temperature and even salinity may influence the period of hatching. High percentages of 'late' eye-pigmentation embryos were observed during early February 1955, in samples off the Suffolk coast and the Wash (Table VII). These would have hatched in late February or early March.

Since hatching takes place during early spring, it is quite probable that adverse environmental factors may influence the recently liberated larvae. The decline in landings of pink shrimps during 1949 and 1950 may have been the result of the very severe winter of 1947, when low temperatures persisted until the middle of March. The destruction of young larvae would influence the commercial catches two years later (Fig. 2).

While examining pump samples taken twice weekly off Burnham-on-Crouch from May until October 1955, for *Crepidula fornicata* larvae, small numbers of *P. montagui* larvae were observed from the beginning of May until the second week of July. Various authors have observed larvae as late as October or November. Björck (1913) found larvae in the Öresund from the middle of July to October. Jackson (1914) found the larvae to be abundant at the surface, but fewer deeper, from 7 to 21 April, off the south end of the Isle of Man. Jorgensen (1923), examining plankton samples taken off the Northumberland coast, from the middle of May to the middle of September, stated that the larvae were rather rare, but the largest numbers were present in July and August. Thorson (1946) found them off Snekkersten, off Ven and off Helsingør from the middle of May to the middle of August. Lebour (1947) stated that larvae occur commonly in the outside waters of Plymouth in spring and summer, with few in autumn; from inshore waters they occur, usually singly, from February to October. Rees (1952) found 67 larvae, during a period of three years, from samples taken from the Forth and Humber regions; larvae were present from March to November, with a distinct peak during April and a secondary peak in August. Since very few ovigerous females have been found after May, and the first eggs are laid in late October or the beginning of November, it is somewhat doubtful whether larvae may be found as late as October. It is possible, however, that the spawning season is prolonged in waters where temperatures are lower than in the Thames Estuary. Jägersten found in the Gullmar Fjord, on 17 July, five specimens which were carrying freshly laid eggs.

Moulting and the loss of the ovigerous setae must take place soon after the liberation of the larvae, as only a small percentage of cemented females, i.e. those with egg membranes and strands of cement attached to the pleopods, was observed during the months of March, April and May. Pike (1952) mentions a period of 10 days from hatching to moulting for *Pandalus bonnieri*. Observations on ovigerous females in the laboratory tanks showed that, during April, the first ecdysis took place after 13 days, but during May moulting took place after 8 to 12 days. In one sample trawled east of Great Nore Tower, river Thames, 3 April, 1952, the percentage of cemented females was 68·0, and most of these females were still carrying a few unhatched larvae in the egg chamber.

Larval stages found in the *Crepidula* samples from the river Crouch measured 2·40 to 4·40 mm. Larvae which had been hatched in one of the laboratory tanks measured from 2·40 to 3·40 mm. total length, i.e. a little more than twice the length of a 'late' eye-pigmented egg. These were measured less than 24 hours after hatching. Eggs from one individual, which were ready to hatch but were still attached to the ovigerous setae and in the egg chamber, were transferred to a small dish and observed through a microscope.

The development of the eggs was not uniform (see Kurata (1955)). Eggs which were on the outer surface of the mass were more advanced and ready to hatch. Signs of life, i.e. beating of the heart, or slight movement of the abdomen, were observed in eggs measuring 1·10 mm. and over, and where complete extension of the abdomen took place the eggs measured 1·20 to 1·30 mm. Since prior to hatching the pleon is flexed under the cephalo-thorax and the telson reaches or overlaps the head of the embryo, the length of newly-hatched larvae must lie between 2·40 and 3·40 mm.

There is direct correlation between size and the number of eggs carried by female pink shrimps (Fig. 8). About 70 shrimps of various carapace lengths, a range covering the smallest

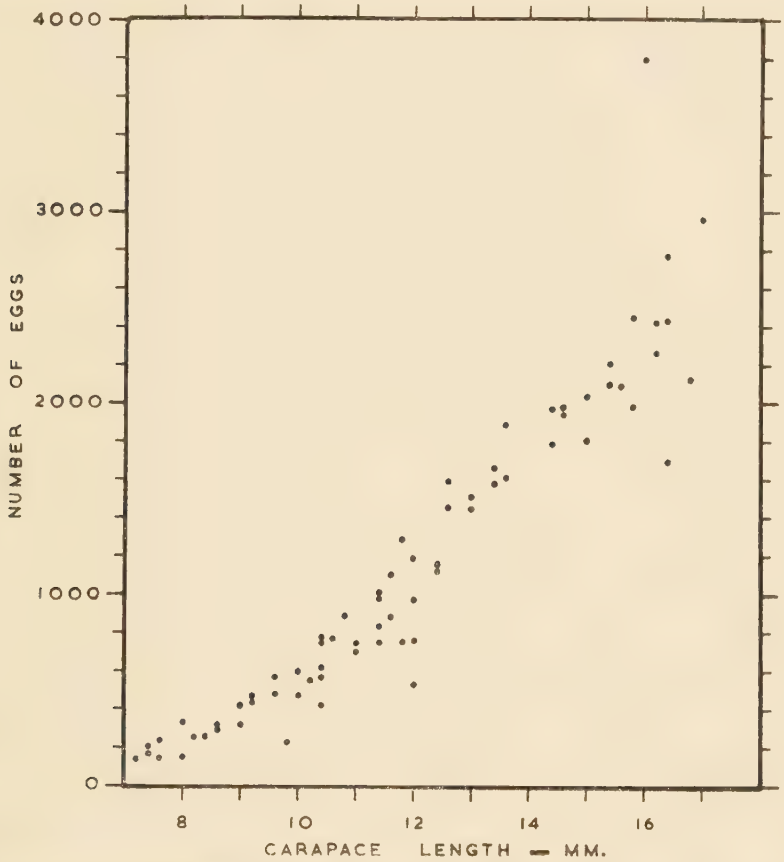


Fig. 8. *The relationship between size and fecundity in* Pandalus montagui. *The individual with a small number of eggs, carapace length* 9·8 *mm. was parasitized by* Hemiarthrus abdominalis.

to the largest ovigerous females found in the samples collected during 1950-52, were examined and the eggs counted. The smallest number of eggs carried was 136 (carapace length 7·2 mm.) and the largest 3,796 (carapace length, 16·0 mm.). The number of eggs carried by the latter was at least 1,300 more than the normal number found in a shrimp of that size, and since variation of about $\pm$ 20% was observed in individuals of a near size-group (carapace length 15·8, 16·4 and 16·8 mm.), it is quite probable that large variations are more common in large than in small shrimps. There was no substantial variation in the number of eggs from specimens of similar carapace length collected during the beginning, middle or the end of the breeding season. The presence of the parasitic isopod *Hemiarthrus abdominalis* causes a considerable decrease in the number of eggs laid, since it occupies a space which would have been taken by the eggs. In a single case of parasitisation (carapace length 9·8 mm.), the reduction was about 50%.

SEX CHANGE

When the samples collected during 1950-51 were measured and sexed, it became apparent that the male secondary sexual characters of the pink shrimp were showing considerable variation throughout the year. Jägersten (1936) and Leloup (1936), who both observed the same phenomenon, arrived at different conclusions. Jägersten maintained that in *P. montagui*, as in *P. borealis*, there are three categories of individuals; the protandric hermaphrodites, the primary females and the secondary females. Those in the first category

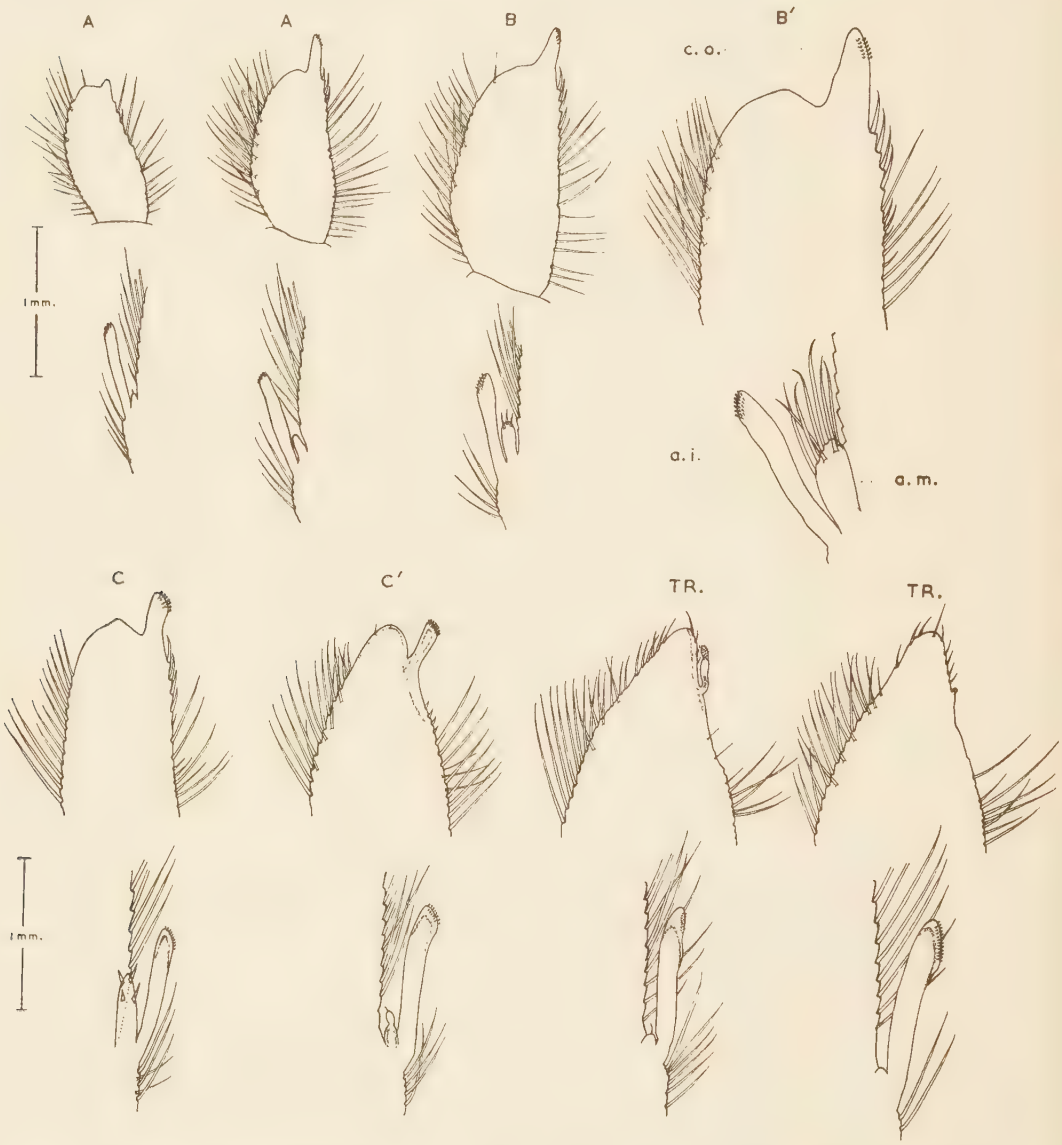


Fig. 9. *Secondary male characteristics of* Pandalus montagui. *Upper series: endopodites of 1st pair of pleopods (c.o. copulatory organ). Lower series: part of the endopodite of 2nd pair of pleopods (a.m. appendix masculina, a.i. appendix interna). Setae on endopodites are pinnate, but shown as bare. A. Immature (July, car. lengths 6·4 and 7·4 mm.). B. Maturing (September, car. length 8·6 mm.). B′. Functional (October, car. length 9·8 mm.). C. Transforming (February, car. length 11·0 mm.). C′ Transforming (May, car. length 12·0 mm.). TR. Transitional (June, car. lengths 12·6 and 14·4 mm.).*

will function first as males. Then a gradual transformation of the secondary sexual characters takes place, closely followed by alterations in the gonad, and these eventually become females and lay their first eggs. The primary females exhibit no indication of male characteristics during their development, while the secondary females, whose numbers are small in the catches, form a transition between the hermaphroditic specimens and the primary females. Jägersten's account of *P. montagui* is short, in contrast to the one on *P. borealis*, and the information given is based on the examination of only four catches. Leloup maintained that his observations on *P. montagui* confirmed the accuracy of the fragmentary morphological facts reported by Calman (1899) and Wollebaek (1908), but contradicted the interpretation given by Jägersten (1935) on the same species, and by Berkeley (1930), and Leopoldseder (1934) on allied *Pandalus* species. Accordingly Leloup maintains that *P. montagui* includes pure females and gynandromorphic males exclusively androgynous. A re-examination of the sex-reversal question was necessary.

The secondary sexual characters of the genus *Pandalus* appear on the endopodites of the first and second pair of pleopods. On the endopodite of the first pleopod there is the copulatory organ (Wollebaek, 1908; Berkeley, 1930; Jägersten, 1936), and on the second the appendix masculina, which serves for holding the female when the males dispose their spermatophores (Leloup, 1936). King (1948) states that the appendix masculina assists to some extent in the handling of the spermatophore. Kubo (1951) and Aoto (1952) do not refer to the inner tip of the endopodite of the first pleopod as the copulatory organ, but as the appendix interna. The development of both these organs has been observed throughout the year on *P. montagui* and for comparison of different samples these have been classified under six stages (Fig. 9). In stage A the copulatory organ appears as a small lobe or tubular projection and the appendix masculina as a small evagination, with or without a thread-like bristle, between the appendix interna and the endopodite. Both organs can be distinguished in young individuals of 5·0 to 6·0 mm. carapace length, but below 4·6 mm. the copulatory organ is not easily distinguished and the whole appearance of the endopodite is not unlike that of a female individual (Fig. 10, A). Below the copulatory organ appear three or four small but strong spinae-setae, in contrast to the long pinnate setae which cover the lateral sides of the endopodite. These strong spinae-setae are absent on the endopodites of female

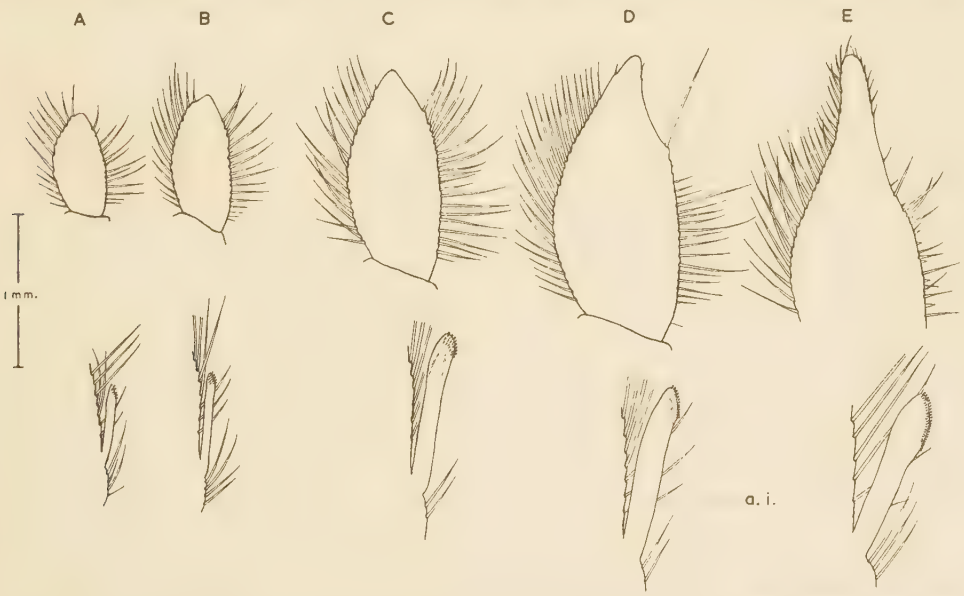


Fig. 10. *Secondary female sex characteristics of* Pandalus montagui. *Upper series: endopodites of 1st pair of pleopods. Lower series: part of the endopodite of 2nd pair of pleopods (a.i. appendix interna). A and B. Immature (July, car. lengths 5·6 and 7·2 mm.). C. Maturing (August, car. length 9·0 mm.). D. Mature (September, car. length 10·0 mm.). E. Mature (June, car. length 12·4 mm.).*

individuals. The appendix interna is found in both sexes, from the second to the fifth pleopod inclusive. In the next stage, B, the copulatory organ is larger and so are the spinae-setae. By this time the appendix masculina carries three or four short strong spines. Simultaneously the small hook-like outgrowths or cincinnuli, on the apex of the copulatory organ, become more prominent (Fig. 9, B). In stage B′, which may be called the 'active' phase, as it is found in males before or during sperm disposition, the endopodite has increased three-fold, and the appendix masculina has become larger, carrying 7 or 8 strong slightly curved spines. After copulation, which takes place sometime in autumn, the male organs start to degenerate. This, however, does not occur simultaneously in all individuals. In stage C the size of the endopodite has decreased, the copulatory organ is smaller and the tip of the endopodite is more pointed. The appendix masculina, although retaining its maximum length, has lost some of its long spines, while those remaining have been reduced considerably in size. This stage could be easily confused with stage B, although the carapace size of the individual, the pointed apex of the endopodite and the length of the appendix masculina should assist in determining the appropriate stage. During the following months the atrophy of the male appendages on the first and second pleopods continues. In stage C′ the copulatory organ and the appendix masculina have decreased further in size and the lateral spinae-setae, below the copulatory organ, have been reduced considerably in size and numbers. The next two stages may be called 'transitional', because the general appearance of the endopodite of the first pleopod is not unlike that of a female. The copulatory organ is either present, its position having been altered by the extension of the apex of the endopodite, or it is only just visible as a small lobe. The spinae-setae have disappeared. The appendix masculina may be present as a small vestige, or completely absent, but still indicating its former position by the apparent space left between the appendix interna and the endopodite (Fig. 9, TR.). However, when the transformation has advanced considerably the appendix interna tends to be very close to the endopodite. There was no definite order with regard to the disappearance or complete absorption of the above two organs. In most cases, however, the appendix masculina was the first to disappear.

The development of the endopodites of the first and second pleopods in the female was found to be without any complications. The distal end of the endopodite of the first pleopod elongates gradually and eventually becomes lanceolate (Fig. 10). The pinnate setae which, in the early stages, cover more or less both sides of the endopodite, gradually decrease in size and numbers on one side. In the second pleopod the appendix interna gradually enlarges, but it is always adjacent to the endopodite at its base. Simultaneously the cincinnuli on the apex of the appendix interna become more prominent and numerous. The ovigerous setae appear before oviposition and disappear with the first moulting after the hatching of larvae.

No other reliable external character on which the sexing of the individuals could be based was observed. Generally the males were smaller and narrower in body, while the females were broader and possessing larger epimera. The latter become deeper before the oviposition and protect the eggs and the abdominal segments. In smaller or larger individuals, however, the above-mentioned characteristics were not so pronounced.

The genital orifices of the pink shrimp were not taken into account for distinguishing the sexes. The oviducts discharge the ova on the inner side of the coxopodites of the third pair of pereiopods, while the male openings are to be found on the coxopodites of the fifth pair of pereiopods. The latter were very difficult to observe and because all the samples examined were preserved in formalin, one could give a different interpretation to these indistinguishable openings.

All samples from the three different stations were treated on the basis of the above classification and it will be seen that the development and transformation of the secondary male sexual characters followed almost identical lines (Fig. 11). Young male individuals, A and B stages, average carapace length 5 to 8 mm., appeared in the catches during the summer months, reaching the active male stage in autumn. Since the percentage of male individuals exhibiting stage B was small, it is considered that the transition from A to B′ stage takes place rather quickly. The stage B′ was retained until as late as February of the next year, when the first signs of transformation appeared. A small percentage of

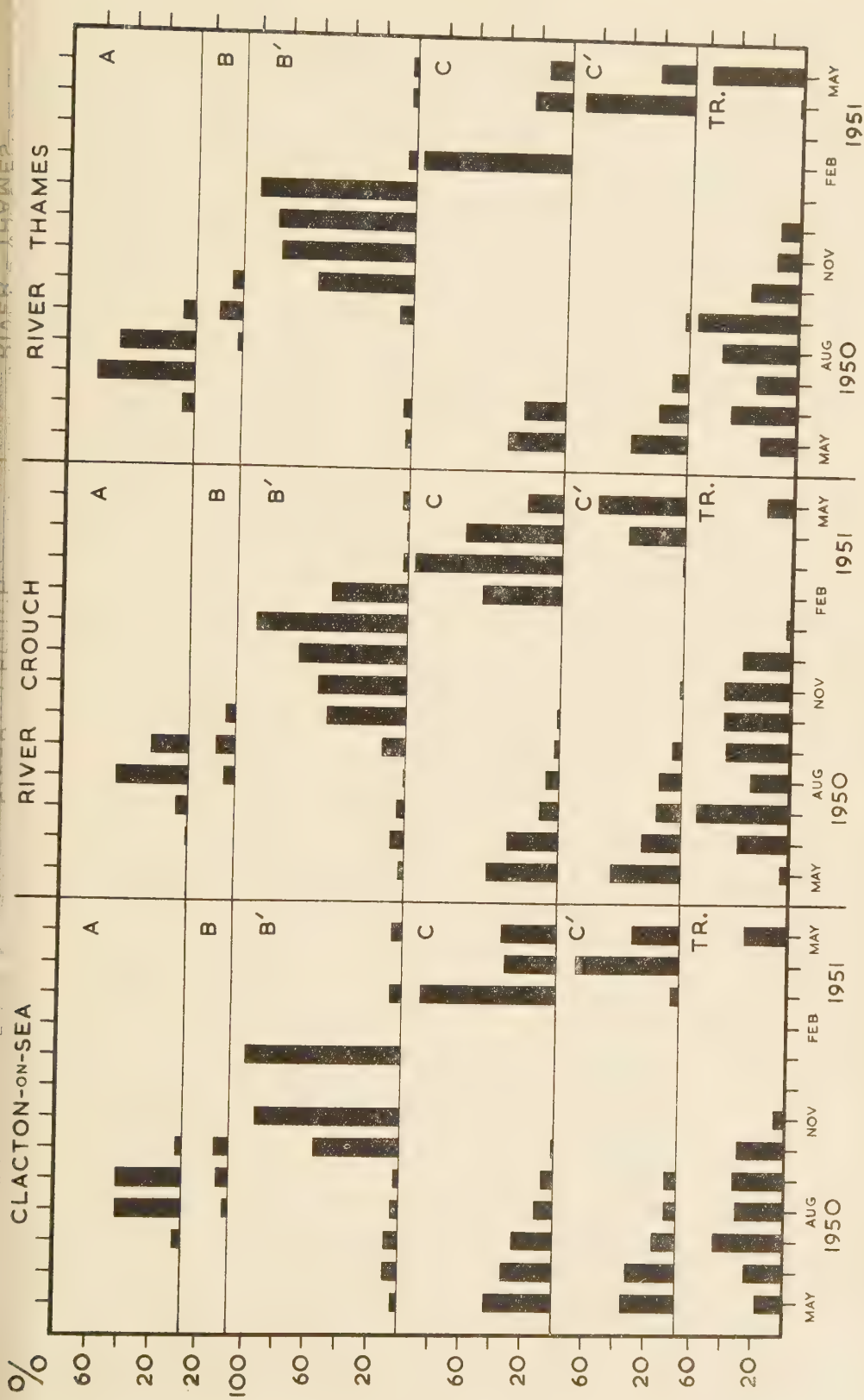


Fig. 11. *Percentages of different stages of development or transformation of secondary male sex characteristics, in monthly samples collected from three different areas during May* 1950 *to May* 1951. *Stages as Fig.* 9.

Table IV: Developing ovaries in transitional individuals during the years 1950, 1951 *and* 1952

Date	River Crouch				Date	Clacton-on-Sea				Date	River Thames			
	Carapace Length					Carapace Length					Carapace Length			
	7–10·8 *mm.*		11–15 *mm.*			7–10·8 *mm.*		11–15 *mm.*			7–10·8 *mm.*		11–15 *mm.*	
	Nos. in sample	*% with develop. ovaries*	*Nos. in sample*	*% with develop. ovaries*		*Nos. in sample*	*% with develop. ovaries*	*Nos. in sample*	*% with develop. ovaries*		*Nos. in sample*	*% with develop. ovaries*	*Nos. in sample*	*% with develop. ovaries*
4 July 50	–	–	49	–	5 July 50	–	–	45	–	25 July 50	16	–	11	–
4 Aug. 50	2	–	34	–	3 Aug. 50	7	–	35	–	24 Aug. 50	13	–	22	–
18 Sept. 50	1	–	54	20·3	6 Sept. 50	10	–	29	10·3	21 Sept. 50	15	–	24	–
16 Oct. 50	1	–	41	34·1	13 Oct. 50	2	–	27	18·5	17 Oct. 50	1	–	21	14·2
9 Nov. 50	–	–	48	62·5	16 Nov. 50	–	–	6	50·0	17 Nov. 50	–	–	7	100·0
8 Dec. 50	–	–	24	83·3	–					18 Dec. 50	–	–	6	66·6
18 Jan. 51	–	–	1	–	19 Jan. 51	–	–	–	–	16 Jan. 51	–	–	2	–
23 July 51	7	–	19	–	16 July 51	2	–	6	–	10 July 51	–	–	15	–
27 Aug. 51	28	–	1	–	24 Aug. 51	11	–	4	–	8 Aug. 51	–	–	20	–
26 Sept. 51	21	–	12	–	27 Sept. 51	7	14·2	10	10·0	–				
26 Oct. 51	6	–	4	–	26 Oct. 51	–	–	3	100.0	9 Oct. 51	3	–	11	27.2
26 Nov. 51	–	–	–	–	23 Nov. 51	1	100.0	2	100.0	7 Nov. 51	2	100.0	10	100.0
–					–					4 Dec. 51	–	–	1	100.0
3 Jan. 52	–	–	–	–	7 Jan. 52	–	–	–	–	21 Jan. 52	–	–	–	–
4 July 52	–	–	121	–										
28 July 52	1	–	36	–										
27 Aug. 52	4	–	29	–										
26 Sept. 52	10	–	32	6·2										
30 Oct. 52	2	–	32	96·8										
28 Nov. 52	–	–	2	100·0										
22 Dec. 52	4	50·0	–	–										

individuals in the active male stage, recognized only by the secondary sexual characters, was present throughout the year, indicating that these males might function twice during their life time. According to Berkeley (1930), *P. danae* spends two years as a male and *P. platyceros* and *Pandalopsis dispar* spend three years in the male phase, and produce sperms in the second and third autumn respectively. It is also possible that these individuals will not undergo the usual transformation until later in their life. It should be pointed out, however, that only a single individual exhibiting fully developed male secondary sexual characters was found of more than 13 mm. carapace length. The transitional stage was reached by May or June, occurring throughout the summer and becoming less and less numerous by the end of December or January, when most probably these shrimps had completely lost their secondary sexual characters and become females. This assumption was confirmed by the discovery of well-developed ovaries, similar to those found in female individuals, on well-advanced transitional and also on individuals still possessing atrophic

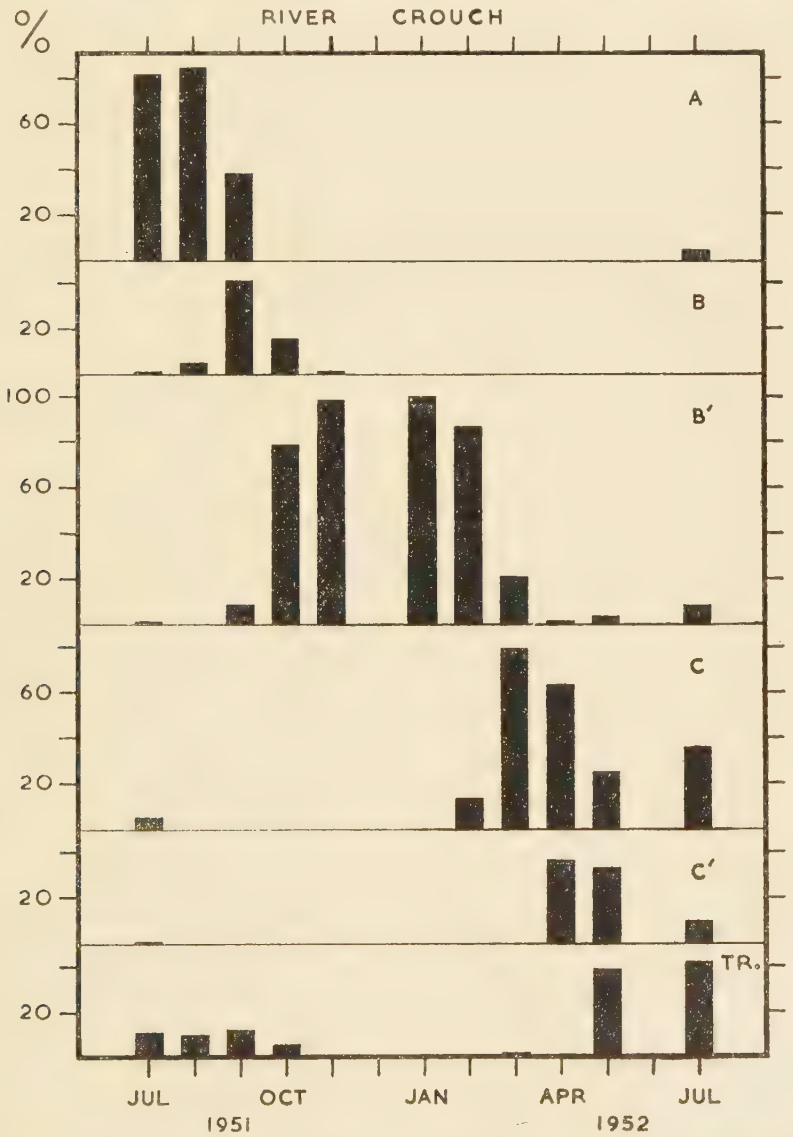


Fig. 12. *Percentages of different stages of development or transformation of secondary male sex characteristics, in monthly samples collected from the river Crouch during July* 1951 *to July* 1952. *Stages as Fig.* 9.

secondary male characteristics (Table IV). A single example with ovigerous setae not fully developed but in stage C′ and with a well-developed ovary was found in a sample collected from the river Crouch on 30 October, 1952 (see Plate 8(b)). It is not unlikely that a small percentage of individuals fails to reach the female stage until the following summer.

The examination of monthly samples, based on the same classification as previously stated, and trawled from the river Crouch from July 1951 to July 1952, showed that the development and transformation of the secondary male sexual characters was similar to that observed during the previous year. The only difference was that smaller percentages of individuals in stages C, C′ and TR. were observed in 1951 (Fig. 12). However, during that summer, samples from the river Crouch and Clacton-on-Sea were mainly composed of individuals of the O-group and consequently these stages were not present.

It will be seen from Table IV that a considerable percentage of transitional individuals showed well-developed ovaries during the months of October and November, approximately at the same time as the female individuals reached the peak of ovarian development (Table II). It was of interest to observe that, in samples collected during the summer and the beginning of autumn, young individuals, approximately 4 to 7 months old, carapace length 7 to 10 mm., exhibited a transitional stage. These individuals possessed a shrivelled copulatory organ, similar to the ones found in advanced transforming males, with or without a very small appendix masculina (Fig. 9, TR.). It is probable that these young individuals, whose presence and abundance varied from one year to another, would never reach the active male stage in the autumn, but would undergo an early sex reversal and become females. A small number of them had well developed ovaries in November and December.

Jägersten (1936) suggested that the secondary females in *Pandalus borealis*, a category of individuals which did not show male characteristics on the pleopods, but which possessed an ovary, vasa deferentia and male orifices, were actual hermaphrodites developing in the male direction, but which for unknown reasons later developed into females. Jägersten found only a few specimens of secondary females in *P. borealis* and *P. montagui*. As the present author has not examined a large number of specimens noting the female and male openings on the third and fifth pair of pereiopods, it is difficult to confirm or refute this suggestion.

To substantiate the hypothesis that the protandric hermaphrodite individuals first function as males, and after passing through the transitional stage eventually become females, it was necessary to observe whether the transformation of the secondary sexual characters closely followed alterations in the gonad. Cross sections of gonads from male individuals in different stages of development or transformation were prepared.

Sections of gonads from individuals which were caught in October and November, and exhibited the 'active' male stage (stage B′), possessed gonads with ovarian and testicular parts. Spermatocytes, spermatogonia and also oocytes were present (Plate 7(A), (B) and C)). Sections of gonads after a period of 6 or 7 months were more informative. In a cross section from an individual caught at the end of May, which was found to be in the first stage of transformation (stage C), the number of oocytes had increased and occupied almost half of the gonad (Plate 7(D)). A section from a bigger individual caught at the same time, but which had reached the transitional stage, possessed a gonad full of well-defined egg cells (Plate 8(a)). It has been mentioned earlier that the process of development or transformation does not occur simultaneously in all individuals. The important section was from an individual caught just before the beginning of the spawning season, whose gonad was full of mature ova (Plate 8(b)), but which still possessed transitional secondary sexual characteristics (stage C′). A section of a gonad from an ovigerous female, captured towards the end of December (river Crouch, 22.12.52), is shown for comparison (Plate 8(c)).

The majority of *Pandalus* species are protandrous hermaphrodites. Berkeley (1930) found plenty of small males, but no small females, when studying the life-history of *P. danae*, *P. borealis*, *P. hypsinotus* and *P. platyceros*. Jägersten (1936), who was unaware of Berkeley's work on the four *Pandalus* species, discovered that *P. borealis* included pure females whose existence was unknown previously. This category amounted to a little less than 5% of all individuals. Tamura (1950), Kubo (1951) and Aoto (1952) stated that *P. nipponensis* and *P. kessleri* exhibit protandrous hermaphroditism, with no small females.

Pruter and Harry (1952) have suggested that *P. jordani* has a life-history similar to those worked out by Berkeley, as they found no small females in the samples collected between the Columbia river and the Rogue river. Two species of *Pandalus* appear to be bisexual, *P. propinquus and P. bonnieri*. Pike (1952) did not observe any protandrous hermaphrodite individuals in the latter.

Leloup (1936), who studied the transformation of the secondary sexual characters in *P. montagui*, did not mention the number of individuals examined. Unusual appearances of the secondary sexual characters from parasitized or unparasitized specimens were described as 'anomalies'. The examination of large numbers of individuals, however, reveals that these 'anomalies' occur regularly. Even in the present investigation, where various phases of the secondary sexual characters were classified under distinct stages, variations were quite common, but all could not be shown. Leloup remarked that from the moment of the appearance of secondary sexual characters, there is never hesitation in determining the sex of a shrimp. This may be only partly true. On examining samples collected from May to July, it was found that considerable numbers of individuals possessed endopodites which were not of the typical female shape, but were nevertheless classified as females. Occasionally it was possible to observe on these endopodites a minute lobe, which was the remnant of the copulatory organ, or that the appendix interna of the second pleopod was not immediately adjacent to the endopodite, indicating that formerly an appendix masculina had been present. These were individuals in the very late transitional stage, and after some time they would be indistinguishable from females. Rarely an individual was found with a typical female endopodite, but possessing a remnant of the copulatory organ.

Leloup, who studied also gonad sections of female and male individuals, admitted that the gonads from male specimens of $\pm 40{\cdot}0$ mm. in length, captured during October-November (a period of sexual activity) were ovary-testes or pure testes, but functioned as

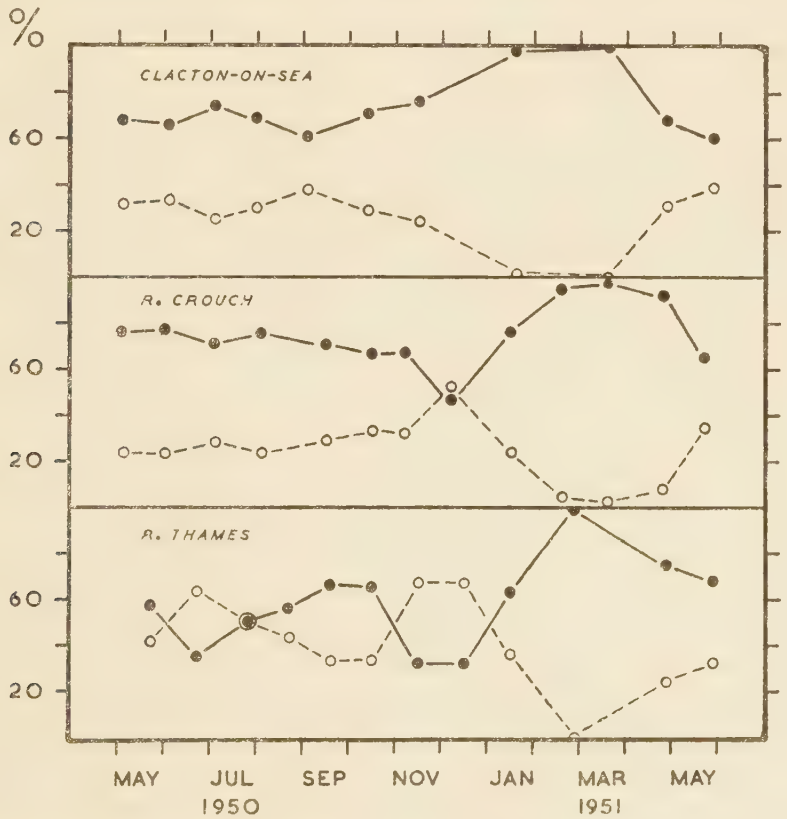


Fig. 13. *Sex ratio in samples of* Pandalus montagui *collected from May* 1950 *to May* 1951. ●—● *Males and transitional.* ○—○ *Females.*

testes. Later the gonads of these individuals which were externally like males, would produce oogonia. Leloup's main argument is that oogonia deriving from male individuals are not capable of perpetuating the species, since none of the specimens examined were carrying eggs on the pleopods. In this investigation no specimens with external male secondary characters were observed to carry eggs. This may be quite improbable, although not impracticable, since individuals reaching that stage would normally have lost their external male characters. However, one specimen which exhibited a late transitional stage, carapace length 14·4 mm., possessed a well-developed ovary, ovigerous setae and a single egg on one of the first pleopods (river Crouch, 8.12.50).

Pandalus montagui is somewhat different from the above-mentioned species in the fact that it exhibits protandrous hermaphroditism, but also includes a considerable number of primary females. Jägersten (1935) suggested that they formed 50% of the population, but this was reduced to between 30 to 35% of the total in his later work (Jägersten 1936).

The examination of monthly samples collected during the period May 1950 to May 1951, from Clacton-on-Sea, river Crouch and river Thames grounds, showed that the percentage of female individuals was not constant throughout the year (Fig. 13). It became larger towards the end of the autumn months, when a section of transformed males would have shown female characteristics and it dropped considerably during the winter months, when there was a tendency for females to migrate to deeper water. This fluctuation was not so apparent in the Clacton-on-Sea area, as no sample was taken during the month of December 1950. The differences shown in the samples from the river Thames can be accounted for by the fact that the stations were quite widespread and varying populations may have been sampled. It is known that populations of pink shrimps move from one ground to another in a very short period (see Migrations). The mean percentages of females caught during the above period from Clacton-on-Sea, river Crouch and river Thames were 26·0%, 25·8% and 41·8% respectively. As the sexing of individuals was based only on the characteristics of the first and second pair of pleopods, and not on the genital openings, it is difficult to suggest what was the actual proportion of primary females.

It is quite probable that these fluctuations of the female to male ratio throughout the year, and the decrease of the female population in *P. montagui* during the winter months, are also to be observed in other areas. Samples of *P. montagui* collected from various localities on the north Wales coast during March 1953, from Menai Bridge to Ormes Head, and sexed by Dr. H. A. Cole, showed that the percentage of female individuals varied from zero to 31·4, with an average for all samples of about 12·5%. This figure is very similar to that obtained during 1952 from samples in the river Crouch (11·31%), river Thames (12·00%) and Clacton-on-Sea (10·66%).

Jägersten's (1936) statement that the primary females constitute 30 to 35% of the total population is considered to be approximately correct. Results obtained from the examination of individuals in the 0-group showed that the percentage of young females varied from 11% to 44%; the majority of samples, however, included 29% to 37% of young females.

GROWTH

It is difficult to ascertain with accuracy the age of crustaceans since there are no suitable organs, i.e. otoliths, scales or rings, to assist in determining their growth. Certain factors should be taken into consideration when studies are made of growth in crustaceans. Offshore and inshore migrations during certain seasons of the year tend to alter the composition of the existing stock. In species where hatching takes place over a long period young individuals will cover a wide growth band. In trawl samples very young individuals may be lost, escaping through the mesh, unless special means are provided to secure them. In the present case, where catches of *P. montagui* were obtained from commercial fishing boats, varying slightly in the mesh of the nets used, the age composition of the catch might differ slightly.

(Photo: P. J. Warren)

A typical 39 *foot Essex 'bawley', with the shrimp trawl hoisted for drying, anchored at West Mersea. When the shrimping season is over, the boats fish for sprats* (Clupea sprattus).

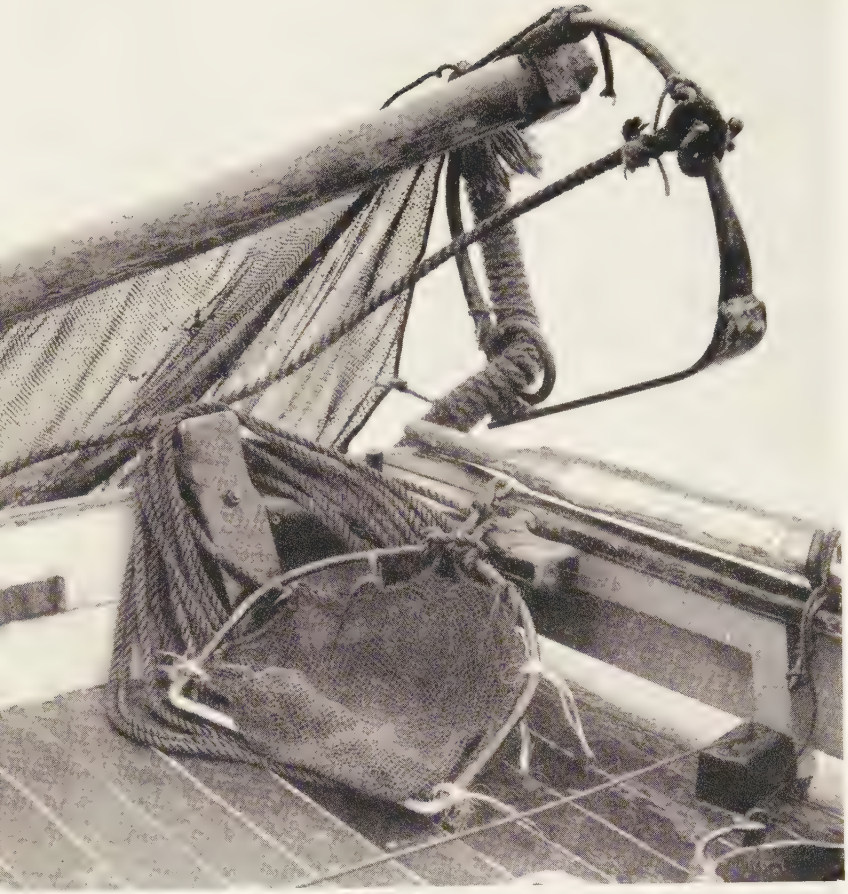
PLATE 1

(Photo: P. J. Warren)

A 31 foot Leigh-on-Sea shrimper. The 'belly' of the trawl is protected by pieces of old shrimp netting.

(Photo: P. J. Warren)

A Leigh-on-Sea shrimper trawling in the river Thames. On the port side can be seen two wooden poles joined by netting, which when fully unrolled are used for drying the cooked shrimps.



(*a*): *Beam trawl ready for shooting. In the foreground is the 'tell-tale'* (*see page* 28).

(Photo: P. J. Warren)

(*b*): 21 *foot oak beam trawl hauled up to a Leigh - on - Sea shrimp boat. The Tollesbury boats use an iron hose-pipe beam. In the foreground the capstan, which is worked from the engine.*

(Photo: P. J. Warren)

(*a*): *The Leigh-on-Sea fishermen protect the ground rope of the trawl by winding around it lengths of* 2 *to* $2\frac{1}{2}$ *inch rope. In the foreground the copper boiler where shrimps are cooked.*

(Photo: P. J. Warren)

(*b*): *The ground rope on Tollesbury shrimp boats is protected by lengths of motor tyres. The cod-end and part of the 'belly' are protected by pieces of inner tubing. Astern the plastic cod-end buoy is visible.*

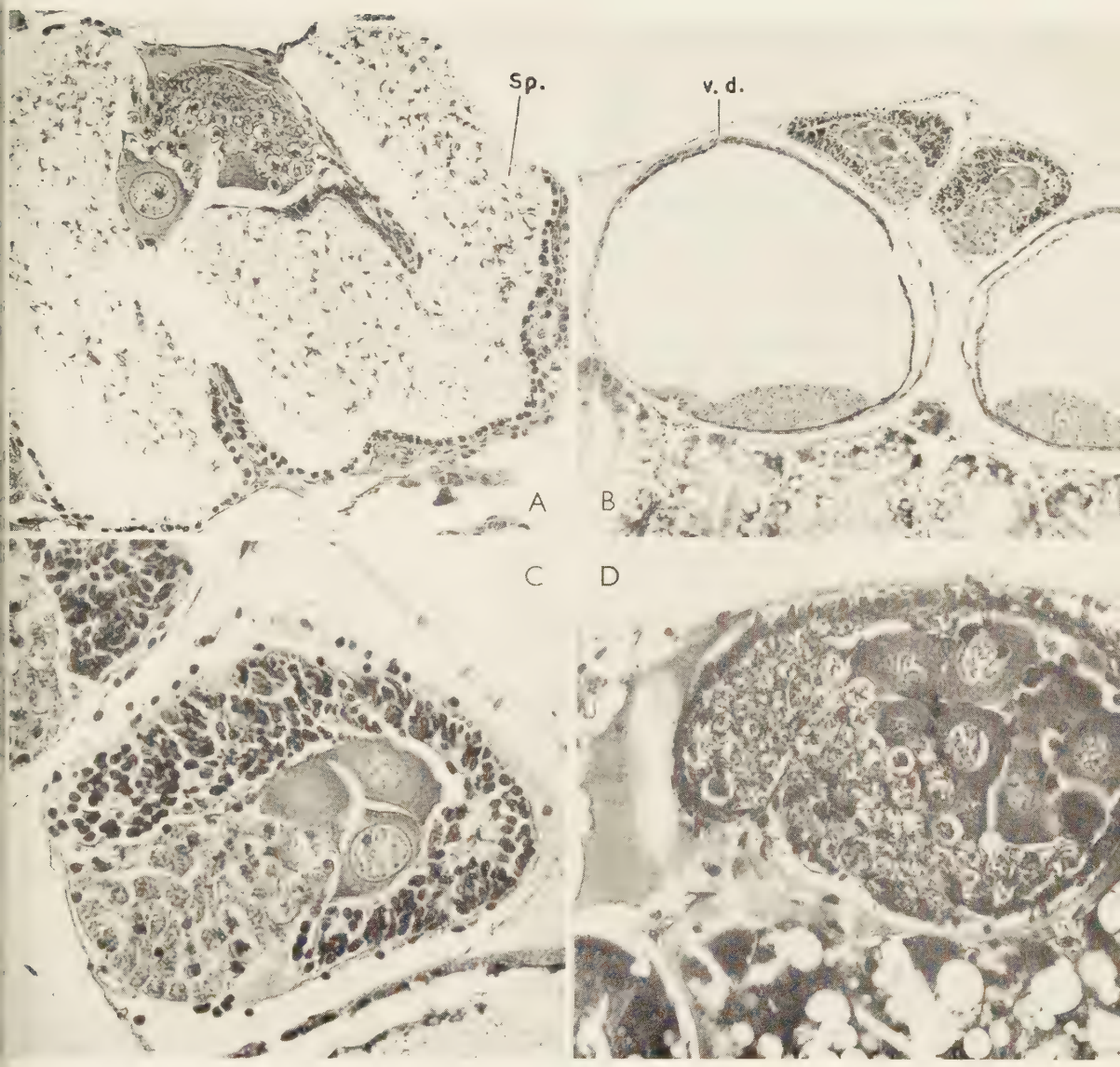
(Photo: P. J. Warren)

(a): A typical pink shrimp catch, with the associated fauna, from a ground south-west of Clacton-on-Sea. The shrimps are put into the riddle for sieving.

(Photo: P. J. Warren)

(b): Cooked shrimps in Tollesbury boats are placed for drying into wooden frames. These frames have a bottom of shrimp netting. The hoop, with which the cooked shrimps are taken out of the copper boiler, and the wire arrangement of the riddle can also be seen.

(Photo: P. J. Warren)

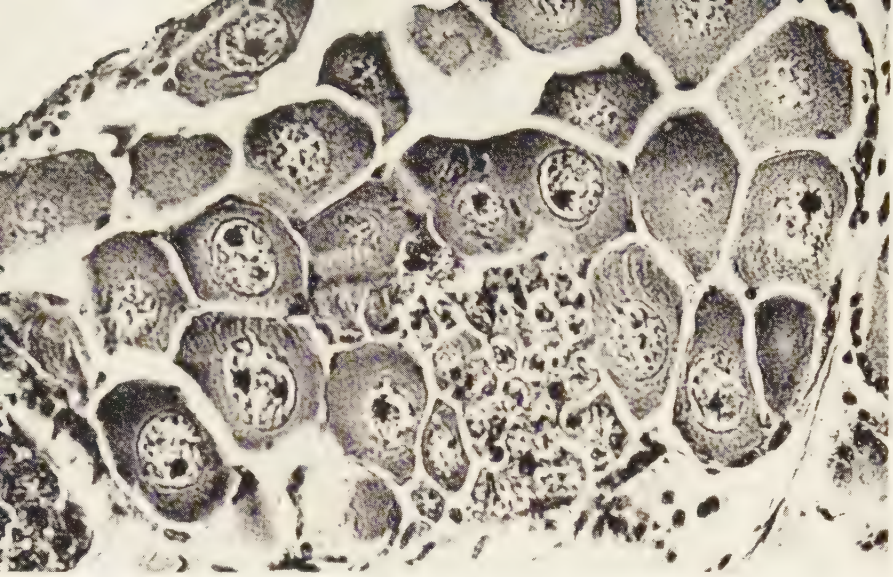


(*A*): *Cross section of a gonad from a mature male* (*stage B′*, 30 *October, car. length* 9·4 *mm.*). *Young oocytes and a single well developed ovum surrounded by spermatozoa enclosed by the follicle cells. Sp., spermatozoa.* (×140).

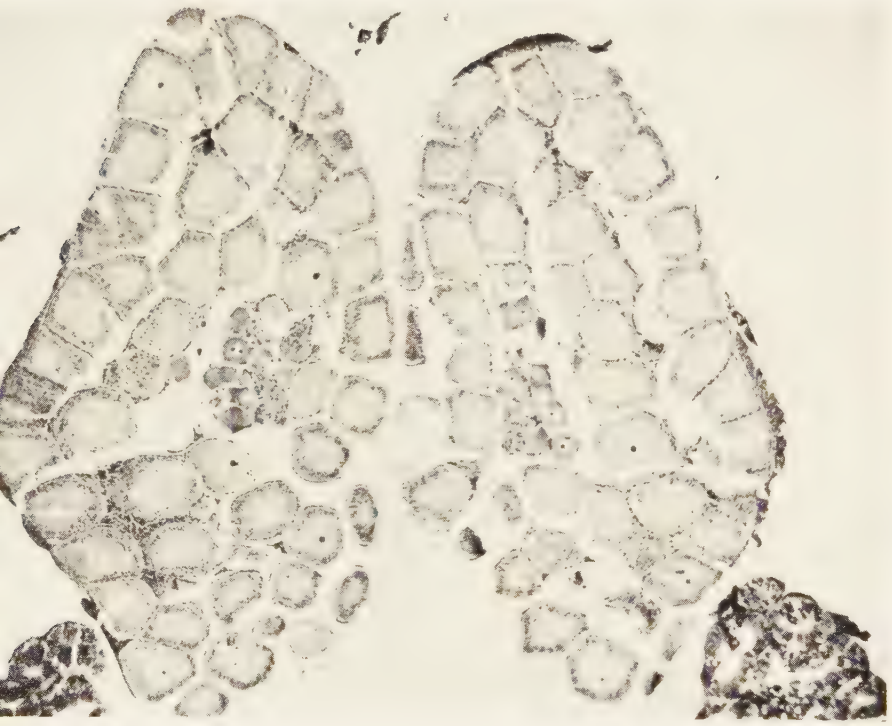
(*B*): *Cross section of a gonad from a mature male* (*stage B′*, 28 *November, car. length* 9·8 *mm.*). *Sperms lie embedded in a sticky secretion in the vasa differentia. Gonad showing oocytes. v.d., vas deferens.* (×65).

(*C*): *Gonad from the same individual, but further enlarged, showing oocytes and three well-developed ova.* (×220).

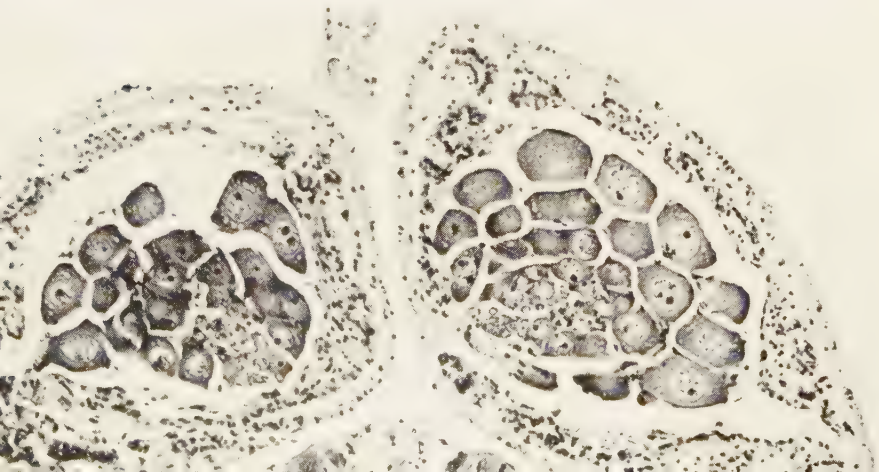
(*D*): *Cross section of a gonad from a transforming male* (*stage C*, 28 *May, car. length* 9·8 *mm.*). *Well-developed ova occupy half of the gonad.* (×220).



(*a*): *Cross section of a gonad from a transitional individual* (*stage TR.*, 28 *May*, *car. length* 13·2 *mm.*). *Lobe of the copulatory organ was still visible on the endopodite of* 1*st pleopod. Well-defined ova occupy the main part of the gonad, with oocytes towards the centre.* (×250).



(*b*): *Gonad of a male* (*stage C'*), *approaching the transitional stage, but still showing male secondary sexual characters* (30 *October*, *car. length* 12·4 *mm.*). *Mature ova occupy the whole gonad, with young oocytes near the zone of proliferation.* (×45).



(*c*): *Cross section of a gonad from a female carrying eggs* (22 *December*, *car. length* 14·4 *mm.*). *Development of a further batch of eggs has commenced.* (×90).

Leloup (1936) states that in *P. montagui* the males live three years and the females four. Jägersten (1936), who considered that the age of the animals could not be judged from size alone, accepted that *P. montagui* lived four years or even more. However, he obtained specimens measuring 9 to 10·5 cm. total length, from the tip of the rostrum to the tip of the telson. No specimen larger than 9 cm. total length was captured throughout the present investigation, and it is assumed that growth in the Gullmar Fjord is considerably quicker than in the southern part of the North Sea. Fox and Wingfield (1937) found that *P. montagui* attained a larger size in the cold waters at Kristineberg than at Plymouth. Wollebaek (1908) found an ovigerous female of total length 160 mm. in the Brevik Fjord, eastern Norway, in about 100 m. depth. Leloup did not give any account of the growth of *P. montagui*, while Jägersten based his observations on only four catches, one of them being too small to be taken into consideration.

In the present investigation catches were obtained more or less at monthly intervals, during a period of two years, from Clacton-on-Sea and river Thames grounds, and for two

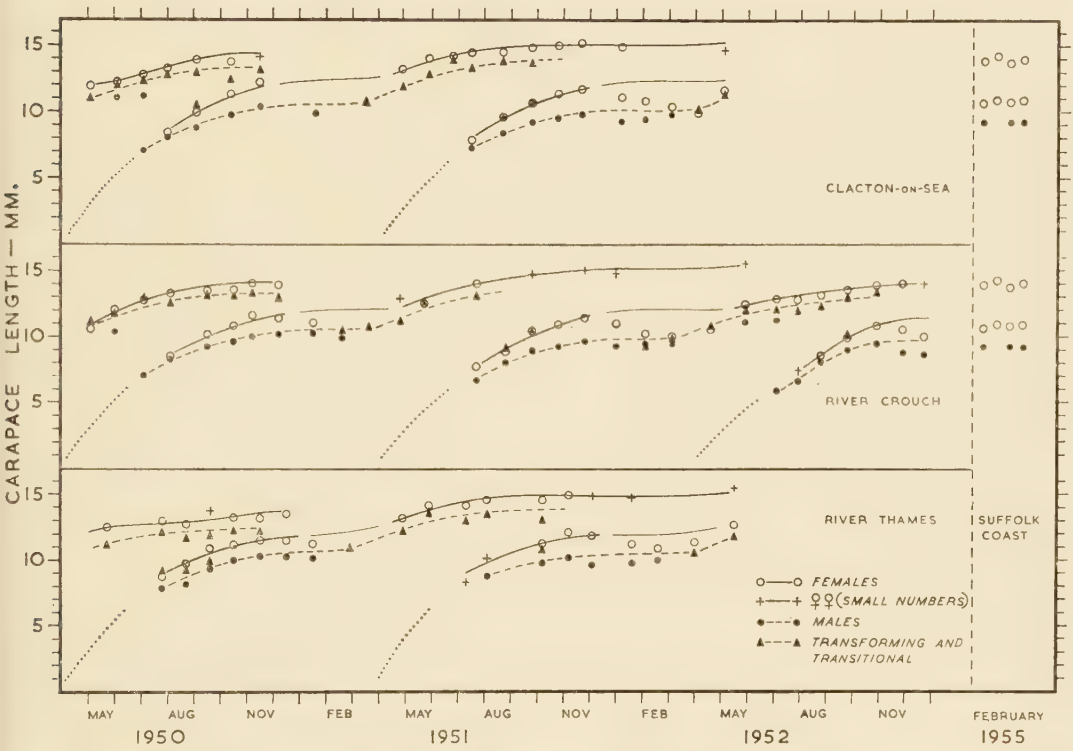


Fig. 14. *Growth in* Pandalus montagui, *based on the measurement of about* 15,000 *individuals.*

and a half years from the river Crouch. Measurements were taken at 0·2 mm. carapace length, but aggregated in 1 mm. groups, and the data obtained on growth are related to the arithmetic means of the age-groups (Fig. 14). The method of employing the arithmetic mean instead of the modal lengths proved to be quite satisfactory where the age-groups were well separated. Difficulty was encountered when the age-groups overlapped, and it is possible that in certain cases some individuals were placed in the wrong age-group.

Jägersten (1936) observed that, in *P. montagui*, growth in the first and part of the second year is quick, but in the third year growth is slight and the second year-class nearly attains the size of the third. The differences between the third and fourth year-classes are insignificant. Jägersten's observations are substantiated by the present investigation, as it proved to be very difficult to distinguish the second and third year-classes, especially of the female populations. Admittedly some distinction could be drawn between the hermaphroditic males belonging to the second and third year-classes, but only at a certain time of the year.

During the months of May and June, when egg-laying has been completed, most of the hermaphroditic males belong to the second year-class and these are in stages C and C′. One can also find at this period a considerable number of large (carapace length 13 to 15 mm.) hermaphroditic individuals which have reached the final stage of transformation. It is possible that some of these larger individuals belong to the third year-class. The differentiation between the second and third year-classes is rather difficult during the following months of summer and autumn, since the two groups overlap and it was decided, therefore, to treat them together. Consequently, unduly high rates of growth may have been obtained for individuals belonging to the second year-class (Fig. 14, May, June, July, 1951).

Growth in *P. montagui* follows more or less similar lines year after year, at least as far as the Thames Estuary populations are concerned. Young individuals, males and females, appear in the catches mainly during the months of July and August, occasionally in June, and grow quite rapidly during the summer months. Growth appears to stop by November and December, the period when the young females will lay their first eggs. When the young individuals normally appear in the trawl catches, they have a carapace length of 5·0 to 9·0 mm. Occasionally smaller individuals of 3·4 to 4·6 mm. carapace length are captured as well, with the commercial mesh-size nets. Since the larvae when hatched have carapace lengths of 0·80 to 0·85 mm., a growth of 3 to 8 mm. occurs during the first two to three months after liberation. As hatching does not take place simultaneously, but may cover a period of two months or a little more, a range of individuals of carapace lengths of 7·0 to 12·0 mm. may be encountered by the end of December. The fact that some individuals can reach carapace lengths of 12 mm. by the end of the first year, can be confirmed by observing the monthly growth and development of the hermaphroditic male individuals. On the whole, female individuals are larger than males, the differences between the two groups being between 0·50 and 1·0 mm. or more, during the summer months. By November or December 80 to 90% of the male population is in the 'active' (B′) stage. Since the largest males of the 0-group have carapace lengths of 11 mm. or over at this period, some female individuals could have attained lengths of 12 mm. and more by the end of the first year.

On several occasions, individuals of 8 to 10 mm. carapace length, belonging to the 1-group, were found in the catches obtained during the months of May, June and July. These individuals were hatched late during the previous year and were still of 7 to 8 mm. carapace length during January, February and March. If their growth during the following months is not rapid, by November or December they may be equalled in size by individuals which have not yet completed a full year. Consequently, the size composition of the first and second year-classes will overlap, thus leading to an overestimate of the growth of the first year class, and high values will be obtained, should the number of individuals in the second year-class be large. This situation may explain the differences in growth obtained for the female population of the 0-group during the years 1950, 1951 and 1952, in the river Crouch. The mean carapace lengths of the females in the 0-group for November 1950, 1951 and 1952 were 11·60 mm., 11·41 mm. and 10·48 mm. respectively. During the summer and autumn of 1952, the 0-group was well separated from the 1 and 2-groups until December. Consequently, the monthly growth increment could be followed without any difficulty, whereas during the autumn of 1950 and 1951, the distinction was not so well marked and higher values were obtained. The monthly seawater temperatures for the river Crouch during the above period did not show any considerable variations to account for any quicker growth during 1950 and 1951. Differences in growth values of the female 0-group were obtained also from samples collected from the river Thames and Clacton-on-Sea grounds during the years 1950 and 1951.

The male 0-group population showed more constant values than the female 0-group, since it was easier to separate males belonging to the 0 and 1-group. The mean carapace lengths of the male 0-group for November 1950, from the three different grounds, were 10·30 (Clacton), 9·95 (Crouch) and 10·26 mm. (Thames), while for November 1951 they were 9·70, 9·58, and 10·15 mm. It follows, then, that the male 0-group population attains carapace lengths of $\pm$ 10·0 mm. by the middle or end of November. As female individuals are usually larger than males by about 1·0 mm. or more, by this time of the year, it is most likely that their mean carapace lengths would be $\pm$ 11·0 mm. Higher values, i.e. 12·25 mm.

for Clacton-on-Sea, November 1950 and 12·12 mm. for the river Thames, November 1951, are the result of some 1-group females being included in the 0-group. In both cases the number of female individuals with carapace lengths of 9·0 mm. or 10·0 mm., was small or negligible.

It was of interest to observe that the monthly growth increment for the female and male 0-groups from samples taken in the river Crouch varied slightly from July to November over a period of three years.

1950			1951			1952		
Date	♀*Increm.*	♂*Increm.*	*Date*	♀*Increm.*	♂*Increm.*	*Date*	♀*Increm.*	♂*Increm.*
4 July			23 July			28 July		
	1·11	1·45		1·11	1·39		1·09	1·41
4 Aug.			27 Aug.			27 Aug.		
	1·69	0·80		1·62	0·90		1·40	0·86
18 Sept.			26 Sept.			26 Sept.		
	0·63	0·30		0·53	0·25		0·89	0·51
16 Oct.			26 Oct.			30 Oct.		

The figures for July-August may be too low due to the loss of small individuals through the meshes of the net.

No similar comparisons can be made for the Clacton-on-Sea and river Thames grounds, as the samples examined were taken from commercial catches, and only for a period of two years.

It will be seen from Fig. 14 that there is a regular downward trend in growth values for the female 0-group after the month of November for all samples, while the growth values for the male 0-group are constant throughout the winter months. It will be observed too that no older groups are shown after the month of December or January. The decrease in growth values in the female 0-group and the disappearance of the later groups is correlated with the offshore migration during the winter months to deeper waters. This explanation was confirmed by the discovery on 10 February, 1955, off the Suffolk coast, at depths of 30 to 40 m., of pink shrimp populations of which 74 to 97% were females, including 95 to 97·5% carrying eggs. The analysis of the four samples which were taken at stations 4 to 5 miles apart, showed that their mean carapace lengths were not unlike those one would expect to find at this time of the year. The mean carapace length values of the female 0-group varied between 10·60 mm. and 10·92 mm., while the mean values of the later groups, 1- and 2-group combined, varied between 13·67 mm. and 14·20 mm. The male population was small, with very few individuals in the transitional stage. The mean carapace length values of male 0-group varied between 9·19 and 9·22 mm. The mean values of these samples are shown in Fig. 14, for comparison with the values obtained from previous years. These values also show that if part of the populations did not migrate offshore to deeper water, the expected growth values would be observed during the winter months.

As a considerable percentage of the female population is carrying eggs during the winter months, no growth is expected until the larvae have been hatched and moulting takes place. The males of the 0-group, however, show signs of transformation of their secondary sexual characteristics and a slight increase in size by March or April, when they will have completed a full year. They continue to grow and at the same time show degenerated secondary sexual characteristics until November or December. During this six month period some hermaphrodite males may have become females, influencing the composition of the female 1-group, while others will not complete their sex-reversal until the following summer. This may explain the higher carapace values obtained for transitional individuals during the months of May, June and July, than rather later during the autumn months. Inshore migration of part of the population, towards the end of the spawning season, may account for the considerable variations in growth values obtained for the female 1 and 2-group during the period of May to July in different years. In the river Crouch, where mixing of

populations in late spring is considered to be slight or to take place later, due to the restricted in-and out-flow of seawater, the mean carapace lengths of female 1 and 2-group shrimps on 2 June 1950, 23 May 1951 and 28 May 1952 were 12·06, 12·60 and 12·40 mm. respectively. However, on grounds situated towards the open sea, mixing of populations would be easier. The corresponding mean carapace lengths for Clacton-on-Sea on 6 June 1950 and 28 May 1951 were 12·27 and 14·02 mm., while for the river Thames on 23 May 1950 and 30 May 1951 they were 12·55 and 14·12 mm. respectively. It appears then that during 1951 there was a considerable influx of older female groups over the whole Estuary, since the mean value for July 1951 in the river Crouch was 14·10 mm., a figure not obtained during July 1950 or July 1952.

Individuals of 16·0 to 18·0 mm. carapace length and over, which are most probably in the fourth year of their lives, were very few and one must make large catches to arrive at a conception of the growth of these older year classes. Only one sample, which was collected from the Inner Dowsing, off the Lincolnshire coast, on 24 April 1955,contained 35 individuals whose carapace lengths ranged from 16·0 to 19·0 mm. It is possible that some of these individuals were four or five years old.

FOOD

Although considerable information is available on the feeding habits of the brown shrimp, no detailed account exists of the food of the pink shrimp. Murie (1903) mentions that ' . . . the East coast shrimpers have long known the principal diet of the pink shrimp is what goes by the local name of "ross" . . . '. Murie refers to this marine sedentary polychaete, which builds the characteristic honeycomb colonies from sand particles, as *Sabellaria alveolata* (*S. spinulosa*)*?*. He states too that ' . . . another allied form of tube-building worm, *Pectinaria belgica*, are great sources of attraction to the prawn shrimps. Their other food is similar to that of the brown shrimp.' He concludes with the statement that the young pink shrimps which are hatched along the parallel sandbanks facing the Essex coast have for safety and food the abundant marine vegetation, the hydroids (*Sertularia*, *Plumularia* etc.), and in addition Foraminifera, minute annelids, molluscs and crustaceans.

Even to the present day the east coast shrimpers believe that 'ross' is a great attraction to pink shrimps. The usual practice is to throw overboard the 'tell-tale' (see Plate 4(a)), a small dredge lined with shrimp netting, which when hauled after four to five minutes drag, will show an indication of possible catch. Live 'ross', with a fair number of shrimps, indicates a good concentration over the ground, while dead 'ross' with a very small number indicates a small or a poor catch. Personal observations confirmed this assumption of possible correlation between concentrations of shoals and abundance of 'ross'. This, however, should not be accepted as a general rule, since on several occasions when live 'ross' was abundant, catches proved to be poor.

The result of the examination of about 650 stomachs, taken at random from the monthly samples trawled from Clacton-on-Sea, river Crouch and Thames grounds, during 1950 and 1951, showed that annelids constituted the main source of food for the pink shrimp, with crustaceans, lamellibranchs and hydroids constituting the remaining diet. It will be seen from Table V that polychaetes constituted 66% to 84% of their food, of which 29% to 52% was definitely 'ross'.

Sabellaria species can be easily distinguished by their characteristic paleae, or special setae, which are found on the operculum. These setae were the only positive proof of *Sabellaria* remains in the stomach contents. Occasionally the complete head with a number of thoracic segments was visible, suggesting that *P. montagui* crawls over the *Sabellaria* colony, cutting off the protruding heads of the sedentary worms. Five stomachs contained two heads of *S. spinulosa* instead of the expected one, although it must be admitted that it was extremely difficult to make any distinction between the two *Sabellaria* species, *S. spinulosa* and *S. alveolata*, since very rarely were the bodies of these annelids found in their entire form. As the majority, if not all, of the characteristic paleae belonged

Table V: Stomach contents of P. montagui *collected during the period, May* 1950-*June* 1951

Fishing Grounds	*Nos. Examined*	*Car. lengths mm.*	*Feeding Individuals*											
			Empty stomachs %	*'Ross'* %	*Poly-chaetes* %	*Crustacea* %	*Lamelli-branchia* %	*Hydroida* %	*Algae* %	*Diatoms* %	*Fat globules* %	*Various* %	*Sand* %	*Silt* %
Clacton	215	9·0–14·9	31·62	52·38	22·44	10·20	8·16	4·08	5·44	1·36	2·04	1·36	36·73	3·40
R. Crouch	210	9·0–14·9	39·04	46·09	38·28	6·25	2·34	8·59	5·46	0·78	3·12	3·12	29·68	7·03
R. Thames	220	9·0–14·9	40·90	29·23	36·92	22·30	10·76	11·53	3·84	–	6·15	1·53	38·46	0·76

to *S. spinulosa* and as *S. alveolata* has rarely been recorded over the fishing grounds, it is presumed that *S. spinulosa* is the dominant species on which pink shrimps feed.

It will be observed that the highest percentage of feeding individuals on 'ross' was found in the Clacton-on-Sea samples, with the river Crouch samples second. Whether *S. spinulosa* is more abundant in the northern part of the Thames Estuary, than in the southern part and the mouth of the river Thames, it is difficult to ascertain. However, results from the examination of 20 stomachs, taken from the monthly samples over a period of one year, showed that the absence of *Sabellaria* ranged from 27% for the river Thames samples to 9% for the Clacton-on-Sea and to 0% for the river Crouch samples. It will be seen, too, that the percentages of individuals feeding on polychaetes generally for the river Crouch and Thames samples are similar, but considerably higher than those from the Clacton-on-Sea ones. It is possible, of course, that a small percentage of these polychaetes were *S. spinulosa* remains, which could not be classified as such, since the characteristic setae were absent.

The Thames samples, on the other hand, showed a higher percentage of crustaceans, lamellibranchs and hydroids. It is not unusual to observe variations in the composition of stomach contents from individuals feeding over different and widespread grounds. Plagmann (1939) has shown that individuals of *Crangon vulgaris* taken at different positions on the Elbe Estuary, from Cuxhaven to Schahörn Island, have a variable diet. Forster (1951) also states that the food taken by *Leander serratus* varies from place to place and throughout the year.

It was of interest to observe that the percentage of individuals with empty stomachs did not vary a great deal between the three different areas sampled. There was also no indication of smaller individuals having a higher percentage of empty stomachs than the larger ones. There was a slight suggestion, however, that shrimps showed some inactivity in feeding during the period preceding oviposition.

During November 1950, when percentages of empty stomachs from the three areas varied from 40·0 to 60·0, out of 31 individuals with empty stomachs, 70·9% had developing ovaries.

Kubo (1951) found that feeding activity in *Pandalus kessleri* was more vigorous during the warmer seasons than during the colder ones, as from April to September the percentages of empty stomachs varied from 18·96 to 38·33, while in January it varied from 66·66 to 87·50. With regard to *P. montagui*, only samples from the river Thames showed higher percentages of empty stomachs during the winter months. In the other two areas, with a single exception, the percentages were not unlike those obtained during the warmer seasons. However, even in the river Thames and Clacton-on-Sea, percentages of 50·0 with empty stomachs were observed during the month of June.

The analysis of the stomach contents shows that pink shrimps, like other decapod Crustacea, do not concentrate on a particular food, but feed simultaneously on a variety of species. Their stomachs generally contained a combination of polychaete worms with lamellibranch larvae, small crustaceans or algae.The percentage containing sand particles was very similar to that of 'ross', since when feeding on *Sabellaria*, the animals were bound to swallow part of the sand-tube. *Pectinaria* sp., which Murie stated to be an attraction for *Pandalus*, has been found in only one individual (river Thames).

The range of food organisms and their relative frequency of occurrence is shown in Table VI.

The percentages of errant polychaetes, for the three different fishing grounds were 14·4, 18·8 and 29·0%, and of these 16·0% to 25% were definitely polychaetes belonging to the Aphroditidae, since their characteristic elytra were present in the stomach.

Remains of the Amphipoda were usually gammarids with carapace cuticles, first or second antennae and several pairs of pereiopods. Of the Decapoda it was possible to identify several remains of small *Crangon* and *Carcinus*. *Hippolyte* and *Pandalus* each occurred once. A few stomachs contained crustacean eggs, most of them being eyed-pigmented and their numbers varying from 1 to 8. Copepods were taken only in small numbers as were cyprid larvae of *Balanus*. However, one stomach contained a newly settled *Balanus* measuring 1 mm. across.

Table VI: Total numbers of various animals taken as food by P. montagui, *from the examination of* 645 *stomachs,* 405 *of which contained food*

	Clacton Total Nos.	*R. Crouch Total Nos.*	*R. Thames Total Nos.*
Polychaeta			
Sedentary (Incl. 'Ross')	93	89	57
Errantia	16	20	25
Unclassified	2	2	4
Crustacea			
Copepoda	–	–	4
Cirripedia	–	1	3
Amphipoda	3	2	25
Schizopoda	1 Mysid 4 mm.	–	–
Decapoda	11	7	16
Mollusca			
Lamellibranchia (*Mytilus*)	20	6	6
Unclassified	3	2	9
Hydroida			
Sertularia	3	2	4
Unclassified	3	9	10
Algae	8	7	5
Tunicata	2	1	1
Foraminifera	+	+	+
Various	1 Fish egg	1 *Crepidula* 2·30 mm.	1 Arm of *Asterias*

It was of interest to observe young *Mytilus* larvae, mainly during the months of March and April, in stomachs of *Pandalus*. The highest number of mussels found in a single stomach was 8, but the majority contained 1 to 3 individuals. The lengths of the young mussels varied between 0·5 and 2·5 mm.

It has not been easy to identify the hydroids found in shrimps' stomachs. Nevertheless, on certain occasions, it was possible to recognize small shoots belonging to the genus *Sertularia*, and on one occasion the shoots belonged to *Sertularia argentea*. Of the unclassified hydroids, several were *Eudendrium* sp., and one was identified as *Sertularella* sp. Of all hydroids found in the stomach contents, 18 to 50% were *Sertularia* species.

Foraminifera were usually present when stomachs contained sand particles. Whether Foraminifera were picked out selectively or were taken indiscriminately was difficult to ascertain. It is possible that they were part of sand-tubes of *Sabellaria* or other sedentary polychaetes.

P. montagui kept in the laboratory tanks were fed with small pieces of *Crepidula fornicata* or *Mytilus edulis* meat and took their food very readily.

MIGRATIONS

CERTAIN decapods have decidedly migratory habits. Havinga (1929, 1930) and Lloyd and Yonge (1947) have described inshore and offshore migrations of *Crangon vulgaris* during the spring and winter months. *Crago franciscorum* and *C. nigricauda*, shrimps found in the Pacific, which are quite similar to *Crangon vulgaris*, move towards the ocean as soon as the spawning season approaches (Israel, 1936). Höglund (1943) and Forster (1951) have also recorded winter and spring migrations of *Leander squilla* and *L. serratus*. Gunter (1950)

mentions seasonal migrations of certain crustacean species in the Gulf of Mexico, especially the "striking seaward movement of *Penaeus setiferus*". Tagging experiments have shown extensive migrations of the larger Georgia shrimp to Florida during the cold season and their return in spring.

Pandalus species also show migratory habits. Wollebaek (1908) states that *P. borealis* makes for shallower localities when the spawn is to be hatched, disappearing from places where they were found in abundance and subsequently returning to them again. Berkeley (1930) had not enough data to determine whether a regular seasonal migration of adult *P. borealis* occurred in British Columbia, as observed in Norway. She states, however, that the larval stages of three deep water *Pandalus* species and of *Pandalopsis dispar* migrate to shallower water in the spring, remain throughout the summer and join the older year-groups in the first winter. No reference is made by Kubo (1951) or Aoto (1952) to movements of *P. kessleri* in the Japanese waters.

Murie (1903) and Kemp (1910) describe *Pandalus montagui* as being gregarious and migratory. Kemp speaks of pink shrimps migrating late in spring to shallower water, where they remain throughout the summer and autumn, and moving outward to depths of 20 to 30 fathoms when females begin to bear eggs on their pleopods. Murie gives a fuller account of these movements in the Thames Estuary. He writes of great shoals making their appearance in early spring " . . . seemingly from the Norfolk and Suffolk coasts, or possibly approach landwards from the deep sea". He considered the latter supposition to be more feasible, as it was supported by statements of the Ramsgate deep sea trawlers and Margate fishermen. The Ramsgate trawlers, fishing during the winter for cod on grounds extending from the Shipwash to the Gabbards, and from Galloper Sand to North Falls and Kentish Knock (Fig. 15), frequently found pink shrimps in cod stomachs and also quantities in the

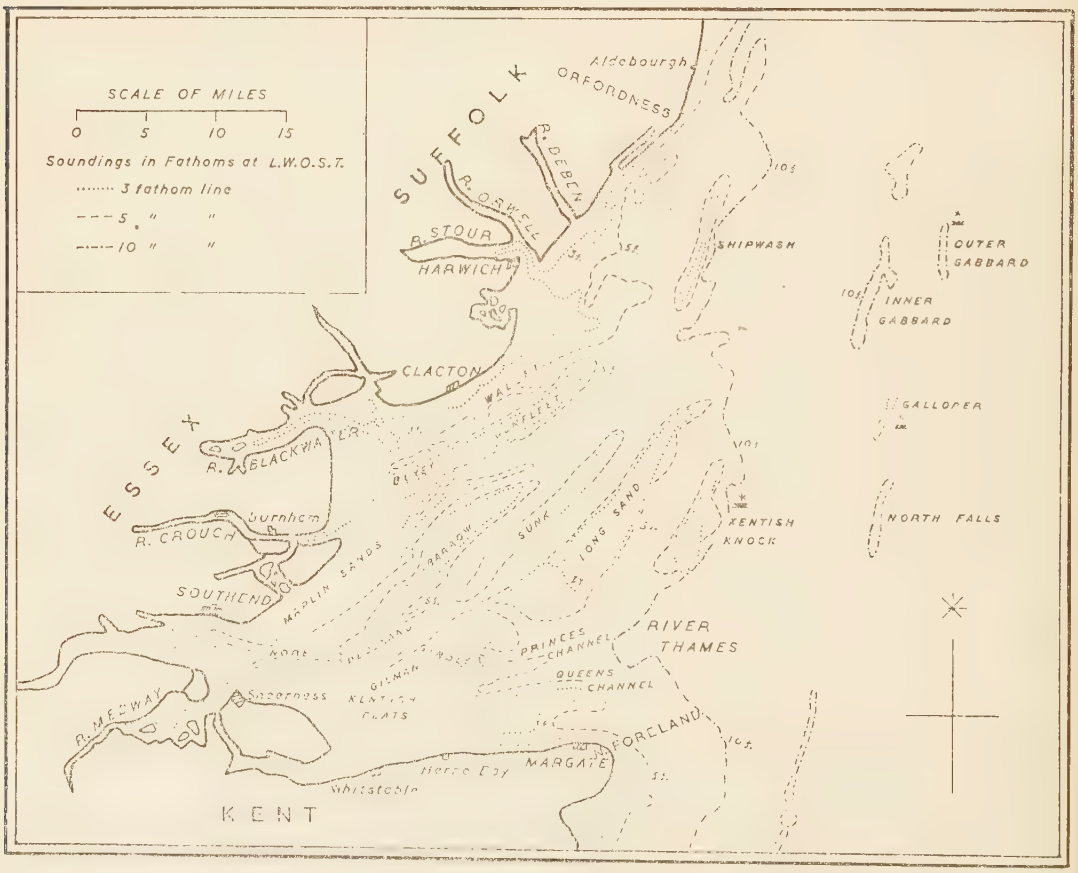


Fig. 15. *Map showing the channels and banks of the Thames Estuary.*

trawls. According to Murie, pink shrimps appear to move in spring from opposite Orfordness towards the Wallet and then to make shorewards and southwards among the various deeps and channels to Prince's and Queen's Channels, where they remain abundant for several weeks. Then they move towards the Girdler, Gilman and Red Sand and still later head up the Thames Estuary, becoming more scattered and mixing with the brown shrimps and even reaching beyond the Nore. According to Murie's account shoals of pink shrimps are found here and there throughout the summer, with their numbers diminishing by autumn. They are still present in small numbers up to the end of November, or even later, if the weather keeps moderate, but by mid-winter they move to deep sea waters, returning in the following spring.

Although it has not been possible to follow closely the movements of pink shrimp populations through the different channels mentioned by Murie, nevertheless our observations support his statement that *P. montagui* appears in the Thames Estuary during early spring and disappears by autumn or even later. Their disappearance, however, is never complete, as small numbers have been found throughout the winter months, in varying concentrations over the whole estuary. In normal years, catches from commercial boats from April to October vary from 7 to 15 gallons or more per hour. The best months are from late April to August. After November the catches drop to 2 to 5 gallons per hour, quantities which are considered to be uneconomic, and fishermen divert their attention to brown shrimps, sprats or white weed. Smaller catches from $\frac{1}{2}$ to 2 gallons per hour were obtained even during the months of January and February 1951 and 1952, from Clacton-on-Sea and river Thames grounds. Increased catches, from 8 to 16 gallons per hour did not materialize until the middle or end of April 1951 and 1952, which suggests that populations of pink shrimps do not migrate inshore earlier than April. In the vicinity of Margate Sands pink shrimps make their appearance in April, but a cold spring may delay them until May.

According to Murie the wanderings of *P. montagui* seem to be in " . . . search of food and procreative instinct". The combined effect of salinity and temperature on movements of certain decapod crustacean species was unknown at the beginning of this century. Balss (1930), who studied seasonal changes and distribution of various decapod crustaceans, stated that marine forms in the tropical zone proceed to the littoral zone in summer because temperatures are higher. In winter surface temperatures are lower and strongly variable and they return to deep water (about 40 m.) with its warmer and more uniform temperature. Caudri (1937), who experimented on the influence of temperature and salinity on the mortality of young *Crangon vulgaris*, found that at a temperature of 4·0°C., the optimum salinity is ca. 34·1‰. Pannikar (1940) stated that in euryhaline species the range of tolerance to dilution of the environment is greater at higher temperatures. Broekemma's (1942) results, on the influence of salinity and temperature on the mortality of *C. vulgaris*, and on the influence of these two factors on the osmotic behaviour of the same species, are most interesting. She found that " . . . with increasing temperature the salinity optimum shifts towards the less saline water", also " . . . with increasing age the optimum shifts towards a higher salinity". With regard to the osmotic behaviour of the brown shrimp, she found that the blood concentration is not independent of the concentration of the external medium and her results explain why " . . . extremely low or extremely high salinities can better be endured when temperature is high". Gunter (1950) shows that the young of both fishes and invertebrates have tolerance for low salinities not possessed in many instances by the adult animals of the same species.

The majority of the existing pink shrimp grounds (Fig. 1) are to be found in depths of 5 to 11 metres (L.W.O.S.T.), with a few grounds (Sheerness Hole, Nore and north of Margate Sand) in depths of 10 to 16 metres. When trawl hauls for pink shrimps were made at monthly intervals, throughout the period of May 1950 to December 1952, temperature and salinity records were taken. Occasional data are also available after January 1953. For a whole year only surface temperatures were recorded, but later bottom temperatures in addition. Observations were made at the beginning and termination of half- or one-hour trawl hauls, as well as after a period of some hours trawling. Most of these variations between bottom and surface were small, usually ranging between $\pm$ 0·05°C and $\pm$ 0·50°C, but on

one occasion a variation of + 2·0°C was recorded after a period of four hours trawling. On grounds situated off Harwich, Clacton-on-Sea, in the river Crouch and in the Thames area, 52 to 76% of the observations showed that bottom temperatures were lower than surface temperatures. Higher bottom temperatures were found in 13 to 30% of the records, while a smaller percentage, from 10 to 22%, showed the same bottom and surface temperatures. Lower bottom temperatures were usually more common on grounds well off land, rather than close to land or where there was a considerable mixing of water through tidal currents. Surface temperatures over three well-separated areas follow more or less the same pattern (Fig. 16). They rise to 18·0°C or 19·0°C during July and August, and fall to 2·0°C, 3·0°C or 4·0°C by January or February. Somewhat higher temperatures are usually recorded in the river Crouch during the summer.

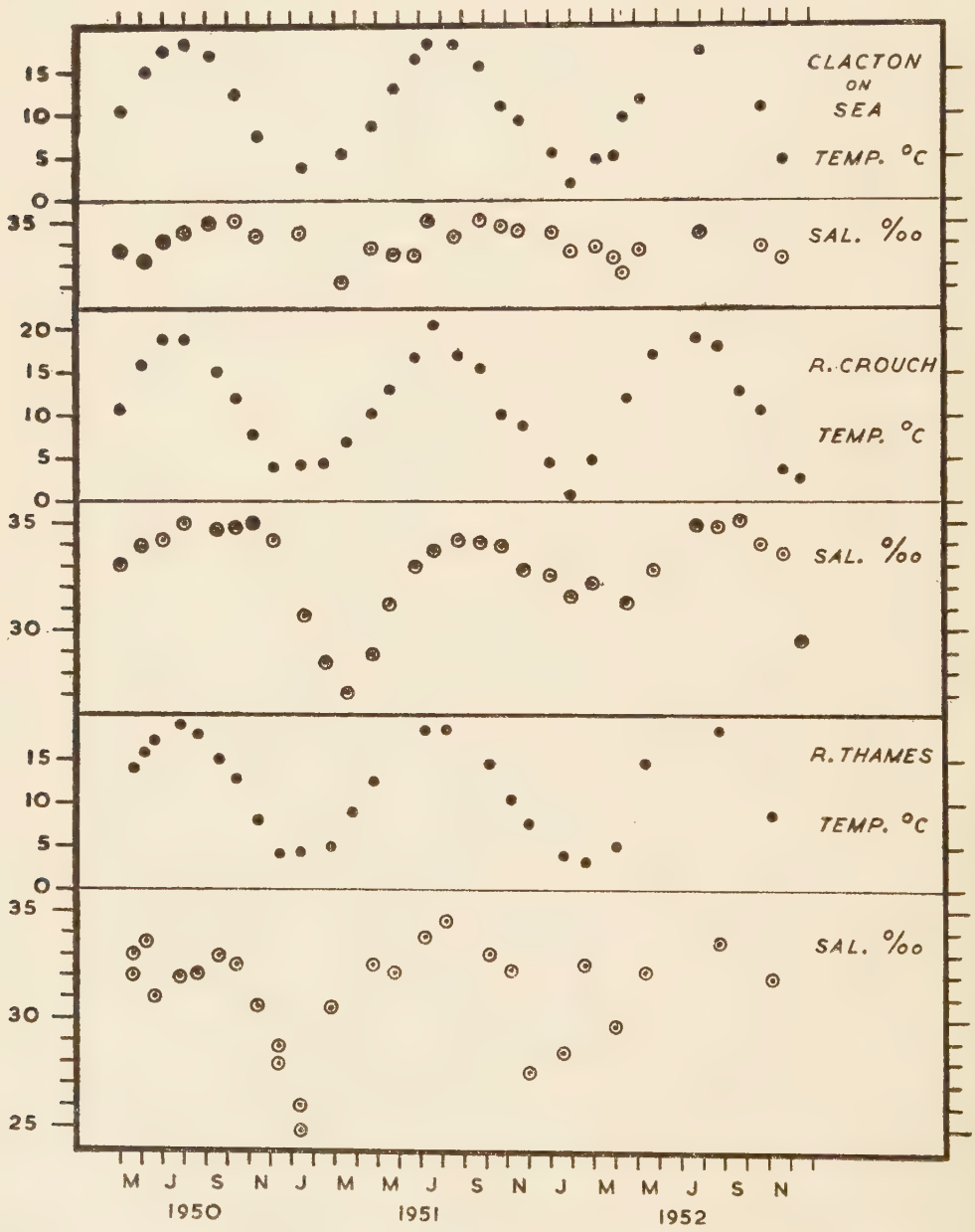


Fig. 16. *Surface water temperatures and salinity records taken while trawling for* Pandalus montagui, *May* 1950 *to December* 1952.

While surface temperatures showed a regular pattern over the whole Thames Estuary, salinity values were not so uniform and variations were encountered from area to area (Fig. 16). On grounds off Clacton-on-Sea, salinities varied between 32·27‰ and 35·30‰, while in the mouth of the river Thames, and in the river Crouch they varied between 24·81‰ and 34·58‰, and 27·12‰ and 35·16‰ respectively. Higher salinity values in the river Thames grounds were usually recorded off the North Kentish coast.

Pink shrimps, in variable concentrations, have been found in all these salinities. Small numbers were found in a salinity of 26·06‰ and still fewer in a salinity of 24·81‰ (January 1951), when surface temperatures were 4·4°C and 4·2°C (Sheerness Hole and Yantlet Flats) respectively. Larger concentrations of pink shrimps were found when temperatures were lower, but salinities higher. On February 20, 1952, a catch of 1·8 gallons per hour was obtained, three miles off Herne Bay, at depths of 4 to 5·5 metres, when bottom and surface temperatures were 3·20°C and salinity was 32·4‰. Also at the beginning of the same month catches of $\frac{3}{4}$ to 1 gallon per hour and 1 to 2 gallons per hour were obtained in the river Crouch and off Clacton-on-Sea, when bottom temperatures were 1·40°C and 2·35°C and salinities 31·59‰ and 33·64‰. Between February 9 and 11, 1954, a very small number of *P. montagui* were found on grounds off Harwich, when bottom temperatures were from 0·45°C to 1·00°C, and salinities from 34·80‰ to 35·23‰. In general during the winter more shrimps are found when temperatures and salinities are relatively high. Catches also increase with depth.

It has been mentioned by various authors that many decapod Crustacea seek deeper waters during the winter months, because temperature and salinities are usually higher than close to land. Although the majority of pink shrimp populations migrate offshore to deeper water after October or November, a small percentage remains throughout the winter over the whole Thames Estuary. Populations which remain usually seek the deeper grounds where food and shelter from wave action are available. This concentration was observed in two successive winters, on a ground off Sheerness (Sheerness Hole), where depths ranged between 9 and 15 metres and where live 'ross' was present. While pink shrimps were very scarce during the winter of 1950-51 on other grounds in the Thames area, a small concentration was present over this ground. During the above period temperatures ranged from 4·2°C to 4·9°C and salinities from 26·06‰ to 30·44‰. Higher concentrations were observed over the same ground during the winter of 1951-52. A catch of 16 gallons per hour was obtained on 4 December, 1951 (bottom temperature 7·70°C, salinity 27·61‰), and a catch of 2 gallons per hour on 21 January, 1952 (bottom temperature 4·10°C, salinity 28·49‰). It should be borne in mind, however, that during the summer of 1950 *P. montagui* was very scarce throughout the Estuary, while during the summer of 1951 it was quite abundant.

The examination of samples collected during the winter months showed certain interesting points. After December, or the beginning of January, the composition of age-groups altered significantly. The older year-groups decreased markedly or disappeared completely. It will be seen in Fig. 14, that *P. montagui* of the 1, 2 and older year-groups were not present after December or January and there was a marked decrease in the mean size of the females of the 0-group, which is considered to have resulted from the migration of the larger females. On certain occasions female pink shrimps were present only in very small numbers during February and March. This pronounced decrease or disappearance of female pink shrimps must be correlated with spawning, since egg laying starts in November and ends by May, reaching the highest peak in January (Fig. 5).

Information from various shrimpers tended to support the view that pink shrimps usually remain longer on grounds off Harwich, and also appear earlier, than further south. Murie stated too that " . . . in spring shrimps appear to steer from opposite Orfordness towards the Wallet and make shorewards and southwards through the various channels". Attempts in the past few years to locate the wintering grounds in the Harwich area were unsuccessful due to the inability of the vessel available to proceed to deeper and open sea.

Early in February 1955, two short exploratory trips were made in the Wash and off the Suffolk coast, with the Ministry's M.R.V. ONAWAY, with the aim of obtaining information on winter migrations in these areas. No conclusive results were obtained from 11 half- or

Table VII: Pandalus montagui *collected in the Wash area and off the Suffolk coast during February*, 1955

Date	*Station*	% ♀♀	% ♂♂ + ♂♀	% *Oviger.* ♀♀	*Egg stages*				*Depth*	*Temperature °C.*	
					% *Blastula*	% *Gastrula*	% *Early eye pigmentation*	% *Late eye pigmentation*	*metres*	*Surface*	*Bottom*
3 Feb. 55	1	–	–	–	–	–	–	–	11–13	4·70	4·00
3 Feb. 55	2	10·85	89·14	36·84	28·5	28·5	42·8	–	14–20	4·60	4·10
3 Feb. 55	3	7·69	92·30	43·75	14·2	57·1	–	28·5	25–29	4·20	4·20
3 Feb. 55	4	3·53	96·46	–	–	–	–	–	22–23	4·80	4·35
3 Feb. 55	5	7·85	92·14	54·54	50·0	33·3	–	16·6	24–25	4·35	4·35
3 Feb. 55	6	–	–	–	–	–	–	–	24–25	4·40	4·35
4 Feb. 55	7	36·66	63·33	83·63	47·8	21·7	17·3	13·0	17–18	4·90	4·65
4 Feb. 55	8	27·50	72·50	78·18	32·5	34·8	23·2	9·3	17–18	4·80	4·50
4 Feb. 55	9	10·07	89·92	53·84	42·8	14·2	14·2	28·5	20–24	4·70	4·40
4 Feb. 55	10	9·90	90·09	70·00	57·1	14·2	28·5	–	24–25	4·40	4·35
4 Feb. 55	11	8·18	91·81	66·66	66·6	–	–	33·3	27–29	4·20	4·20
10 Feb. 55	*a*	–	–	–	–	–	–	–	25–29	4·45	4·50
10 Feb. 55	*b*	80·66	19·33	97·52	47·0	35·2	13·4	2·5	25–30	4·80	4·60
10 Feb. 55	*c*	97·50	2·50	97·43	14·7	32·1	24·7	28·4	33–35	4·60	4·55
10 Feb. 55	*d*	74·00	26·00	97·29	20·4	38·9	24·0	16·6	28–29	4·60	4·60
10 Feb. 55	*e*	84·00	16·00	95·23	29·1	30·0	25·8	15·0	27–40	4·60	4·60

one-hour trawl hauls made in Lynn Deeps and east of the Wash as far as the Haisboro' Light Vessel (Fig. 17). The quantities taken were very small, varying from 0·25 to 0·45 gallons per hour in Lynn Deeps to N.E. Docking Buoy, and from 0·15 to 0·9 gallons per hour east of Burnham Flats. East of Burnham Flats the number of *P. montagui* decreased gradually towards the Haisboro Light Vessel. Surface temperatures ranged from 4·20 C to 4·90°C, and bottom temperatures between 4·00°C and 4·65°C. Salinities ranged between 31·55‰ and 34·18‰, being higher towards the open sea, and depths varied from 11 to 29 metres (Table VII). Information was obtained on the nature of the bottom, where hauls were made, by employing an ordinary oyster dredge, with teeth on the blade, and lined with shrimp netting. Colonies of 'ross' were found on only four stations, and with one

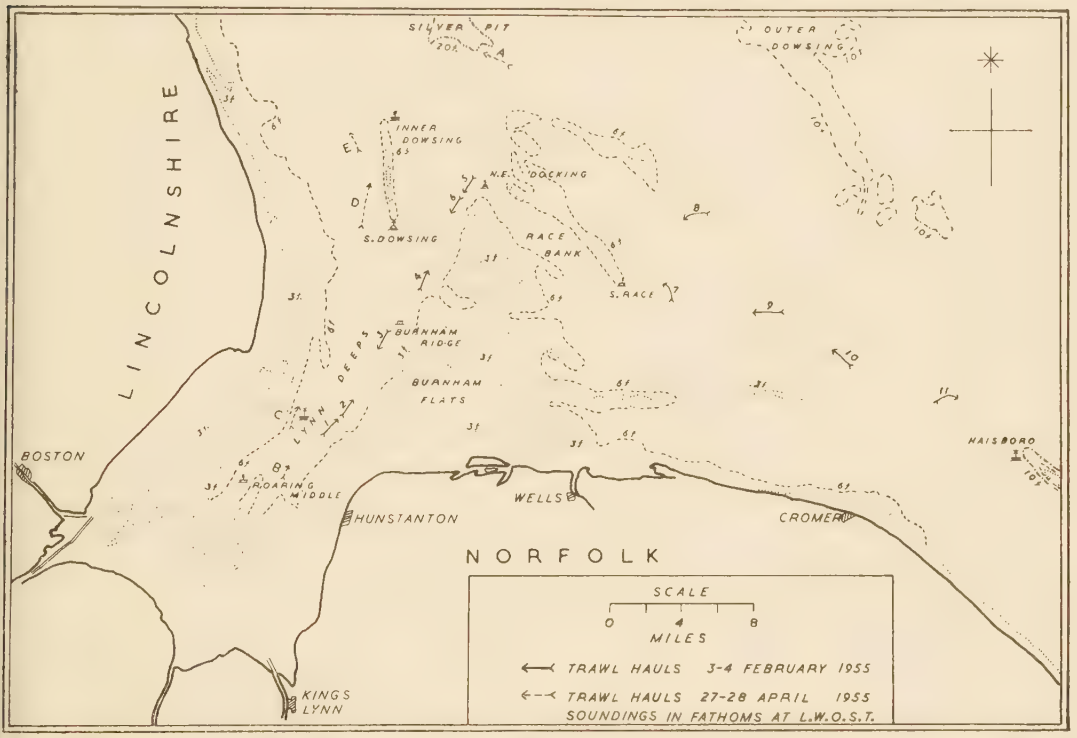


Fig. 17. *Map showing the Wash area, where trawl hauls were made during February and April* 1955.

exception the colonies were dead. It is assumed that *P. montagui* populations in the Wash either disperse over a wide area, during the winter months, or migrate to grounds which have not been located and where food is abundant.

Results obtained from half- or one-hour trawl hauls on February 10 from five stations which covered a line from south east of Lowestoft to 3 miles south east of the Shipwash Light Vessel, yielded very interesting results. Stations were approximately 8 to 9 miles from the coastline and 4 to 5 miles apart (Fig. 18). Surface temperatures ranged between 4·45°C and 4·80°C, and bottom temperatures between 4·50°C and 4·60°C (Table VII). Salinities ranged from 34·25‰ to 34·33‰ and depths between 25 and 40 metres. Considerable concentrations of pink shrimps, approximately 8 gallons per hour, were found only at station *c* (E. 1°51′0″, N. 52°11′12″), while north and south of this station densities decreased gradually, being in the region of 0·6 to 0·9 gallons per hour on stations *b* and *d* and almost nil on station *a*. No pink shrimps were expected at station *a*, although 5 pink and 50 brown shrimps were taken in the trawl, as the bottom was sand with large quantities of *Spisula* and *Cardium* shell. Similar bottom conditions, but with less shell, were found at station *b*, but some dead colonies of 'ross' were found. Unusual quantities of live 'ross', with colonies of up to 12 cm. in height, and large numbers of *Pilumnus hirtellus* and *Porcellana longicornis*

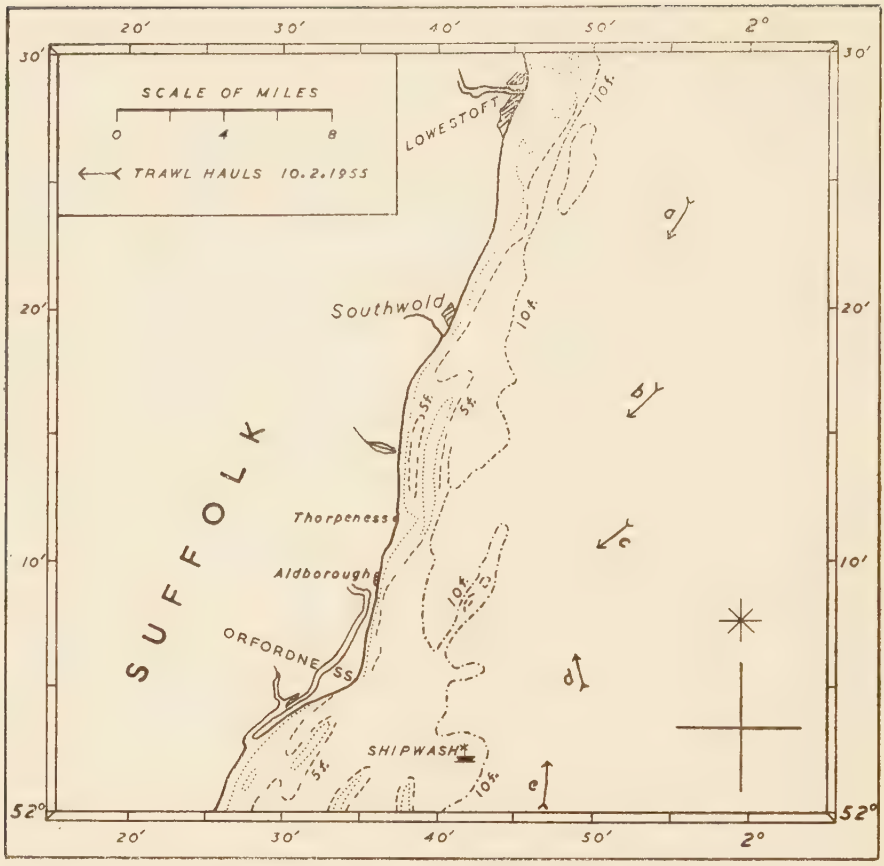


Fig. 18. *Map showing the Suffolk coast and positions where trawl hauls were made in February 1955.*

were found at station *c*, where the largest concentration of pink shrimps was obtained. Further south, colonies of live 'ross' were less common and pink shrimps were obtained in small quantities. It was evident that when *P. montagui* populations seek the deep waters during the winter months, they concentrate on grounds where food is readily available.

The analysis of samples collected from the Wash area and off the Suffolk coast showed that there was a difference in the composition of populations (Table VII and Fig. 19). With the exception of two samples, stations 7 and 8, the Wash catches showed a low percentage of females, 3·53 to 10·85, while the Suffolk coast samples showed a high percentage of females, varying between 74·00 and 97·50. There were also differences in the age-groups, the Suffolk coast samples containing a high percentage of older females. Such low percentages of female pink shrimps during the months of February or March are characteristic of samples collected on the Thames Estuary grounds, when females have migrated to deeper water. During February 1951 and 1952, samples collected on grounds off Clacton-on-Sea, river Crouch and river Thames, showed female percentages varying between 1·00 and 16·00, 5·17 and 19·44 and 0·97 and 12·00 respectively. It is evident then that the bulk of the pink shrimps in the Wash area do not disperse over a wide area, but migrate to grounds which have not been located. It is possible that they move towards the Outer Dowsing grounds, since samples from stations 7 and 8 (Fig. 17) contained female percentages of 27·50 to 36·66. As the Suffolk coast samples showed such high percentages of females, with still higher percentages of ovigerous females (95·23 to 97·52) it is evident that one of the wintering grounds of the populations fished from the Essex ports is situated around station *c* (Fig. 18).

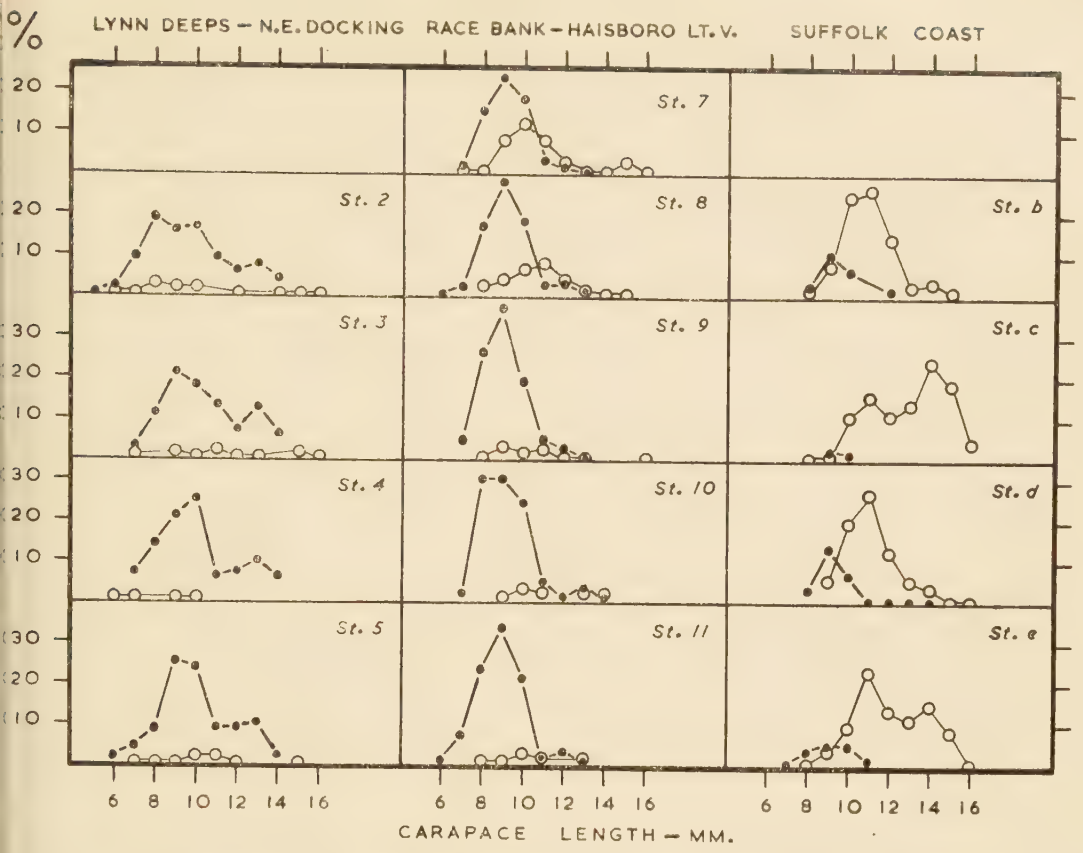


Fig. 19. *Composition of samples of* Pandalus montagui *trawled off the Norfolk and Suffolk coasts during February* 1955. ● — ● *Males.* ○ — ○ *Females.*

A considerable proportion of ovigerous females, from both areas, possessed eggs in 'early' or 'late' eye-pigmented stage. Since percentages of 'late' eye-pigmented eggs were considerably higher than those found in February 1952, in the Thames Estuary, it is possible that either variations occur in the egg development from year to year, or that hatching, which takes place soon after the 'late' eye-pigmented stage is reached, is earlier off the Suffolk coast and in the Wash, than in the Thames Estuary.

Results from a short exploratory trip in the Wash area, in the last week of April, 1955, showed that considerable concentrations had by then appeared on the usual fishing grounds. A catch of 7 gallons per hour was obtained with a 24 foot beam trawl near the south eastern tip of the Inner Silver Pit, and a catch of 8 gallons per hour north west of the South Dowsing Buoy (Fig. 17, Hauls A and D). Smaller catches were obtained with a small 6 foot beam trawl on grounds in the Lynn Deeps. Salinities were in the region of 32·22‰ to 33·91‰, lower inshore, and surface temperatures between 6·70°C and 8·90°C, higher inshore. Percentages of female shrimps were high, between 35·22 and 40·66, being higher on offshore grounds, and showed that female shrimps were returning from their wintering grounds. The sample from station A contained 8·19% of ovigerous females, the others nil; 60·0% of the ovigerous females possessed eggs in the 'late' eye-pigmented stage, while 40·0% possessed eggs in the process of hatching. The remaining female population (51·61 to 76·78%) had ovigerous setae, but no eggs, showing that the larvae had been recently hatched. Higher percentages of females with ovigerous setae were found on stations towards the open sea, which again suggests that hatching takes place before the shrimps move inshore.

No marked differences were observed between the fauna from the grounds trawled in the Wash and those off the Suffolk coast. With the exception of a few additional species of

Crustacea, Mollusca and Echinodermata (*Meganyctiphanes norvegica*, *Crangon allmanni*, *Philoceras fasciatus*, *Pilumnus hirtellus*, *Astarte montagui*, *Calliostoma zizyphinum*, *Trochus truncatus*, *Henricia sanguinolenta*), the fauna was very similar to that found on grounds in the Thames Estuary. Almost all shrimp catches contained variable percentages of brown shrimps, *Crangon vulgaris*, mostly 2·0 to 6·0 with a few samples between 15·0 and 42·0. *Crangon allmanni* (the channel-tailed shrimp), was also found in variable numbers. It was more common in samples from the Suffolk coast than in the Wash. *C. allmanni*, which is very similar to the brown shrimp, but turns to a yellow-orange colour when boiled, has been recorded occasionally from grounds off Clacton-on-Sea and three miles off the river Crouch mouth. Murie (1903) also found a few specimens near the Nore ground (river Thames).

In addition to the offshore and inshore migrations during autumn and spring, *P. montagui* exhibits less pronounced migrations during the summer months. Fishermen, in the Wash or Thames Estuary, speak of finding large concentrations of pink shrimps on a particular ground, but by next day the ground may be barren. Mr. R. A. Dolby, a Leigh-on-Sea shrimper, informed the author that during June 1953, on a ground off Whitstable, he obtained a catch of 80 gallons in one haul, while the previous day another boat had obtained 25 gallons in one haul over that particular ground. But, next day, when nine boats were trawling over the same ground, they did not catch any pink shrimps. Shoals of pink shrimps were located after a period of several days on another ground, several miles further east. Again they were found in large concentrations. Six boats, trawling astern of each other, were obtaining catches of between 36 and 60 gallons in one or two hauls.

Shoals appear to gather on a restricted part of a ground, for on many occasions shrimpers speak of two boats trawling at a speaking distance, one boat obtaining 50 to 60 gallons and the other only 4 to 8 gallons. This gregarious tendency of *P. montagui* may account for catches above 100 gallons per haul. In the second fortnight of 1952, a record haul of 200 gallons in eight minutes was obtained by a Southend shrimper, on a ground off the north Kent coast (*Fishing News*, 1952).

It is most probable that during the summer months shoals congregate on particular grounds for feeding purposes. Such unusual concentrations of pink shrimps must graze down all the available food over a short period. To estimate the number of pink shrimps in one gallon, about 70 counts were made from catches obtained from early April to late November. The shrimps were unsieved and uncooked and were placed in measures of one or two pints and the number found multiplied by 8 or 4. Considerable variations were found. The lowest number per gallon was 1,496 and the highest 5,472. Usually more shrimps per gallon, 2,960 to 4,000, were found during early April, before the older age-groups entered the Estuary, and during August 2,700 to 5,472, soon after the 0-group appeared in the commercial catches. Fewer shrimps per gallon, between 1,496 and 2,472, were found during the months of May, June and July. If the counts made during early April and August are discounted, then the average number per gallon is approximately 2,020 and the average for all counts 2,618. Catches then of 80 to 100 gallons per haul, during the months of May to July, must contain anything between 160,000 and 200,000 shrimps or more.

In the summer of 1955 a great reduction was observed in the catches of pink shrimps over the whole Thames Estuary. Previously very good catches were obtained, but after the middle of July the shoals started to disappear from the normal fishing grounds, and only shrimps of the 0-group were to be found. It is probable that the disappearance was due either to shortage of food, or to the exceptionally high water temperatures which prevailed during the summer months. During August and September 1955, water temperatures in the river Crouch, off Clacton-on-Sea and off Felixstowe were about 2°C higher than during the same period of 1954.

It was of interest to observe that catches of 30 minute hauls made over the same grounds, river Crouch and off Clacton-on-Sea, from July until November 1955, increased when water temperatures dropped gradually. On July 14 and 15, 1955, bottom water temperatures in the river Crouch and off Clacton-on-Sea grounds were 20·15°C and 19·40°C respectively. Catches per 30 minute trawl hauls varied between 0·9 and 2·0 gallons, and 1·3 and 3·2 gallons. By the middle of August, bottom temperatures were 18·10°C and 17·35°C on the

two grounds respectively, and catches varied between 1·1 and 3·1, and 2·3 and 7·2 gallons per 30 minute hauls. On 15 September 1955, bottom temperatures in the river Crouch had dropped by 20·0 C, and catches varied between 3·0 and 5·5 gallons per 30 minute hauls. By 11 October 1955, although bottom temperatures had dropped in the river Crouch to 13·0°C, catches did not become smaller but were 1·4 to 6·3 gallons per 30 minute hauls. Smaller catches of 0·9 to 2·5 gallons per 30 minute hauls were obtained on 11 November 1955, in the river Crouch, when bottom temperatures were 9·0°C, and the first ovigerous females had appeared in the catches. This decrease in catches suggests that *P. montagui* populations in the river Crouch moved to offshore grounds after the middle of October. On 27 October 1955, when temperatures varied from 11·10 to 10·6°C, four 30 minute trawl hauls off Clacton-on-Sea yielded catches from 4·0 to 8·1 gallons, considerably higher than those obtained earlier in the month from the river Crouch. By the end of November, when bottom temperatures dropped by 3°C, catches off Clacton-on-Sea dropped by approximately 50%.

It has been observed that *P. montagui* does not survive for long periods in laboratory tanks. The longest period of survival was approximately 40 days, during April to May, when tank water temperatures were 10·9°C to 13·0°C. During the summer months *P. montagui* perished in a period of two to three weeks. Müllegger (1950) had also observed that *P. montagui* succumbed in warmer water in aquaria, and it was impossible to keep them alive when water temperatures rose above 16 to 17°C.

Fox and Wingfield (1937) stated that *P. montagui* and *P. borealis* which are found in the Gullmar Fjord with an annual temperature range of 5°C to 7°C, could not be kept alive in an aquarium at 11°C. At Plymouth, however, where the water temperature rises to 15°C in summer, *P. montagui* can be kept alive in an aquarium at 17°C. They have also demonstrated that the heart beat rate and the oxygen consumption increase with rising temperatures.

PARASITES

The bopyrid isopod *Hemiarthrus abdominalis* (Krøyer), was the only parasite observed on the pink shrimp. It was usually found attached beneath the anterior part of the metasome, on one of the first pair of pleopods. Bate and Westwood (1868) recorded its occurrence on *P. montagui* on the Sussex coast in 1846. Sars (1899), and Nierstrasz and Brender à Brandis (1926), state that it parasitizes several species of *Spirontocaris* and a few *Pandalus* species. Leloup (1936), who found several individuals of *P. montagui* parasitized by an isopod, did not mention its identity. It is most probable that this parasitic isopod was *H. abdominalis*. He did observe, however, that parasitized individuals of *P. montagui* showed abnormal pleopods; a few male individuals possessed one female and one male pleopod. Leloup states that temporary or permanent parasitization causes the females to reach the adult form more rapidly, while feminizing the males. Baffoni (1947) found that the main effect of parasitization on male *Eupagurus prideauxi* was the appearance of typical feminine pleopods.

The percentage of parasitized pink shrimps in the Thames Estuary is considered to be small. The examination of 73 samples, collected over a period of two and a half years, and with a total number of 25,000 individuals, showed that only 22 samples included a small number of infected *Pandalus*. The percentage of parasitization varied between 0·22 and 2·53, with the river Crouch and Clacton-on-Sea samples showing the highest percentages. *Hemiarthrus abdominalis* was more common in samples collected during May, June and July, less common during the winter and spring months, but totally absent during the autumn months.

The total number of parasitized *P. montagui* was 78, of which 69 were female and 9 male individuals. The infected females did not show any striking abnormalities in their secondary sexual characteristics. Two ovigerous females had a smaller number of eggs than that of equal size females, since the space occupied by eggs was taken by the parasite. Of the

9 male individuals only one showed abnormal pleopods. It possessed one typical female endopodite and one male endopodite. Since the male individual was only of 6·4 mm. carapace length, it was apparent that the presence of a parasite was suppressing the secondary male characteristic at an early stage. The remaining males were in the final transitional stage or in the transforming stage, and with the exception of one individual they possessed carapace lengths of 10·0 mm. to 11·6 mm., which indicates again an early suppression of the secondary male characteristics.

The parasites were either females or females with one male attached to the ventral face of the metasome. Females containing eggs in their marsupial cavity and with one male, or females with eggs, but without a male, were found only from February to June, but mainly during May and June. Possibly the small males may have become detached during preservation. The males were small, 1·5 mm. to 2·3 mm. in length, the females measuring 3·5 mm. to 9·0 mm. According to Sars (1899), the female parasite attains a length of 11 mm., and the male a length of 3 mm.*

Parasitization of *P. montagui* by *H. abdominalis* varies from area to area, and it is possible that it varies over a period of years. From May 1950 to May 1951, the annual parasitization rates in samples collected off Clacton-on-Sea, rivers Crouch and Thames were 0·59%, 0·56% and 0·16% respectively. During the period of June 1951 to June 1952 the annual parasitization rates from the same areas had dropped to 0·05%, 0·26% and 0·03% respectively. Samples of *P. montagui* collected between 3 and 25 March 1953, from positions off the North Wales coast, showed variations from zero to 11·1%, while the majority varied between 4·3% and 5·9%. A series of pink shrimp samples collected during the early part of February 1955 from stations off the Norfolk and Suffolk coast (Figs. 17 and 18), showed considerable variations. The percentage of parasitized shrimps in samples taken off the Norfolk coast varied from 2·32 to 7·33, while those from the Suffolk coast varied between 0·66 and 1·33. In the Firth of Clyde, Scotland, parasitization of *P. montagui* averages 10·2% (Pike, in the press). It appears that parasitization is higher in northern waters than in southern. Pike states that the intermediate host of *H. abdominalis* is *Pseudocalanus* spp.

Until the samples from the Wash and off the Suffolk coast were examined, it was considered that usually only one male was attached to a female parasite. However, in a sample taken south east of S. Race Buoy (Fig. 17), it was observed that two males were attached to a female parasite carrying eggs in the marsupial cavity.

In samples collected from river Crouch and off Clacton-on-Sea, during July 1955, four specimens of *P. montagui*, carapace lengths 11·0 to 15·0 mm., were carrying between 25 and 60 specimens of *Balanus*. These were 0·7 to 1 mm. in length, and with the exception of a few barnacles on the first metasome segment, the majority had settled on the carapace, on both sides of the rostrum.

DISCUSSION

Sex reversal or protandrous hermaphroditism occurs in certain groups of crustacea, cirripedes, parasitic isopods and also in certain species of mollusca, e.g. *Crepidula fornicata* (Conklin, 1898; Orton, 1909), *Patella vulgata* (Orton, 1928), *Patella coerulea* (Bacci, 1948). The great majority of decapod crustacea, however, are bisexual, with certain species, e.g. *Lysmata seticaudata* (Spitschakoff, 1912; Dohrn, 1950), *Calocaris macandreae* (Runnström, 1925) exhibiting functional hermaphroditism. Species belonging to the genus *Pandalus* show a high percentage of sex reversal.

The distribution of the genus *Pandalus* is world wide, and at least thirteen species have been recorded. Of these only two species are bisexual, *P. propinquus* (Jägersten, 1936), and *P. bonnieri* (Pike, 1952), while seven species show sex reversal. In the remaining three species described by Brian (1942), *P. martius*, *P. narwal* and *P. heterocarpus* there is no mention of sex ratio. *P. montagui* exhibits similar internal and external transformations to

*A female parasite of 11 mm. was found in a sample from Fleetwood, 3 July, 1956.

P. borealis and other *Pandalus* species, with the difference that primary females are more numerous and therefore the tendency towards protandrous hermaphroditism is less pronounced than in other species.

The causes that produce sudden changes in *Pandalus* species are not well understood; there is a possibility that changes in the hormonal balance may be responsible. Leloup (1936) considers that the transformation in the internal medium of the animal probably arises from a synchronous modification of the external physico-chemical medium. He concludes that the seasonal increase of the dissolved salts in the seawater, notably phosphorus, may have an effect on the sexual organs, phosphorus determining the speed of their formation.

Growth in Crustacea and particularly in shrimps, cannot be determined precisely. Growth data derived from frequency distributions and given in the present investigation must be considered as tentative only and indicative of growth rates over the period of two and a half years of the investigation.

Burkenroad (1951) states that repeated samples in the same locality do not represent the same population, as young individuals are usually added in a given part of the range, while at the same time older individuals emigrate. " . . . . The rates of mortality and addition of new individuals seem so high for shrimps, that it would hardly be satisfactory even to sample the whole population, and weight the length-frequencies according to changes in distribution . . ." Burkenroad advanced the method of measurement of growth-rate from natural rates of moulting and of increase in size per moult; (a) from percentage of soft-shelled individuals in samples captured, and (b) from frequency of shedding in captive samples during the first day or so. Burkenroad suggests that despite the difficulties and complications of this method it offers a relatively favourable approach to this problem.

Even if Burkenroad's method could be applied to certain *Penaeus* species, or other caridean shrimps, it is questionable whether it could be applied to *P. montagui*. This species dies after a short period in tanks, especially during the summer months, when ecdysis will be most frequent. Mortality was very high even among specimens brought into the laboratory tanks, and which had previously been placed in a vessel, with frequent changes of water, as soon as the catch was emptied on deck.

Growth in *P. montagui* is quite rapid during the first 6 or 7 months. Growth rates of the 0-group must be studied with a certain amount of caution, since the nets used were most probably not capturing all the young individuals which entered the population during late June, July or August. Although individuals of 3·4 to 4·0 mm. carapace length were captured by the nets employed, it is most likely that a considerable percentage of these young individuals escaped through the mesh, and consequently the catch did not contain any but the larger individuals of the 0-group.

P. montagui does not grow as large as other *Pandalus* species, and it is questionable whether growth rates can be compared. Some comparison could be made, however, with *P. bonnieri* which attains carapace lengths of 21 to 22 mm. (Pike, 1952). While individuals of *P. bonnieri* with such lengths were quite frequent in samples collected in the Clyde, the largest recorded *P. montagui* was 19 mm. carapace length, and the majority of large individuals were between 14 and 16 mm. The breeding season of *P. bonnieri* is also similar to *P. montagui*, the first and last ovigerous females being present from the end of October until the middle of April. In addition the first *P. bonnieri* larvae appear in late February or the middle of March, a little earlier than *P. montagui* larvae appear in the Thames Estuary. Pike (1952) has shown that by July male and female *P. bonnieri* of the 0-group have carapace length of 3 to 5 mm., and by December or January 10 to 11 mm. While mean carapace lengths for *P. montagui* during July appear to be higher than those of *P. bonnieri*, mean values for the period December 1950 to December 1952, from widely collected samples, varied between 8·75 and 10·30 mm. for males, and between 9·92 and 11·83 mm. for females. It is apparent that some similarity exists in growth rates between these two *Pandalus* species. This similarity in growth rates does not continue during the following years, as growth in *P. montagui* is retarded considerably. Female individuals of approximately 3 years of age have carapace lengths similar to those attained by *P. bonnieri* in a period of 18 to 20 months. Duration of life appears to be similar in both species.

Verwey (1949), reviewing the relations between marine animals and selection of habitat, stated that while fixed animals are closely bound to the substratum with ". . . a more or less complicated innate series of actions . . .", in mobile animals certain species show a distinct preference for certain types of bottom, and if this is not available the species may inhabit all other kinds of bottom, and consequently the animals are loosely bound to the substratum. *P. montagui* is usually found on hard sandy bottom, with variable quantities of small to medium sized stones, and shell. The type of bottom may be suitable for the settlement of *Sabellaria spinulosa*, and *P. montagui* seeking particularly this food are attracted by its presence. Hjort and Ruud (1938), and Bigelow and Schroeder (1939), found that abundance of *P. borealis* was correlated with the supply of organic debris on the bottom. Hildebrand (1955) noticed pronounced differences in the fauna of pink shrimp (*Penaeus duorarum*) grounds and the neighbouring brown shrimp (*Penaeus aztecus*) grounds in the Gulf of Campeche. *P. montagui*, however, feed also on various other animals, amphipods, lamellibranchs, hydroids, which may be found at some distance from typical *Sabellaria* grounds. Small numbers of *P. montagui* have also been taken by ordinary oyster dredges, from oyster grounds in the Essex rivers, which are known to have muddy bottoms. The majority, however, are found on well-defined grounds, and some relation exists between substratum and the distribution of *P. montagui*.

Balss (1930) stated that migrations of decapods are usually associated with propagation, although they may result from other motives, such as change of temperature and lack of food. Caudri (1937) and Broekemma (1942) have shown the importance of the combined effect of salinity and temperature. Broekemma has found from laboratory experiments with *Crangon vulgaris* that the salinity optimum depends on temperature. Newly hatched larvae and one year old shrimps withstand lower salinities better than older individuals, at spring and summer temperatures. The salinity limits for normal development of the eggs likewise depend on temperature. Results also of the influence of temperature and salinity on the osmotic behaviour of the brown shrimp, showed that the internal concentration depends on salinity and temperature of the external medium. If the combinations of salinity and temperature factors have such influence on the behaviour of the brown shrimp, and explain the distribution and migration of the species (although Broekemma admits that all the facts are not sufficient to give a complete explanation), it is quite possible that the above factors have an even greater influence on *P. montagui*, which in contrast to *C. vulgaris* is not an euryhaline species.

Salinities and temperatures usually decrease with the approach of winter, the period when spawning begins in *P. montagui*. While lower salinities are not so harmful as when combined with higher temperatures, the shrimps must seek the optimum conditions; these may be found offshore, in deeper water, where salinities are higher. Verwey (1949), discussing the migration of the shore crab and shrimp (*C. vulgaris*), stated that they may be guided by salinity or both salinity and temperature. " . . . The outward migration of these animals on the approach of winter is therefore physiologically so to speak a migration towards higher salinities . . .".

The desire, however, for outward migration must be more pronounced in ovigerous and older individuals since populations which stay on the grounds after January are usually composed of males and young individuals. The animals move offshore towards higher salinities and temperatures, which are also beneficial for the development of the egg and the newly hatched larvae. This may explain the observation of higher percentages of 'early' and 'late' eye-pigmented embryos in samples taken off the Suffolk and Norfolk coasts during early February 1955, than in samples from the Thames Estuary during early February 1952.

Although decreases in salinity and temperature may influence the outward movement in *P. montagui*, nevertheless small concentrations have been found in the Thames Estuary throughout the winter months. These were usually found on grounds at greater depth where food was available.

The behaviour of *P. montagui* in the Wash area is apparently somewhat different from that exhibited in the Thames area. Pink shrimps are usually found in the former until the end of December and, if temperatures do not drop to very low figures, fishing is continued

until the middle or the end of January. The shoals will then disappear and will not make their reappearance until the end of April. In a recent survey between 6 and 8 December 1955, *P. montagui* was present in dense concentrations on grounds extending from Roaring Middle to South Dowsing and Burnham Ridge Buoys (Fig. 17). 'Ross' was available over these grounds and catches varied between 100 and 150 gallons per hour with 24 ft. beam trawls. One is inclined to accept that hydrographical conditions are not quite similar to those in the Thames Estuary. Although no records of salinities and temperatures are available for long periods from the deep channels in the Wash, it appears that salinity does not drop to levels similar to those obtained from the Thames area. The Wash is comparatively open and there is considerable exchange of water with the North Sea. It will also be noted that these grounds are found in depths between 24 and 40 m. Such depths are normally found only well outside the existing Thames fishing grounds and in such deep areas temperatures will be a little higher than closer inshore. In addition, when food is available, the pink shrimp populations in the Wash may well defer their migration to other grounds until the arrival of very low temperatures.

SUMMARY

1. The pink shrimp (*Pandalus montagui* Leach) is found in considerable densities in the Wash, Thames Estuary and Morecambe Bay.

2. The total annual landings in England and Wales of pink and brown (*Crangon vulgaris*) shrimps fluctuate between one and a half and two and a half million kilograms. The beam trawl is used exclusively for shrimping, the size of beam varying between 18 and 24 feet.

3. The pink shrimp is distributed throughout the Thames area, but it is found in considerable numbers only on certain grounds, and mainly during the late spring and summer months. The pink shrimp prefers hard bottom, where 'ross' (*Sabellaria spinulosa*) is present.

4. Between May 1950 and December 1952 about 25,000 specimens were measured and about 15,000 sexed. Specimens were measured from the base of the eye notch to the posterior mid-dorsal edge of the carapace, since in many preserved samples the rostrum is damaged and the abdomen flexed. The approximate total length of a shrimp can be found by multiplying the carapace length by 4·5.

5. The ovaries begin to mature in early August, but the peak of development is not reached until November-December. The breeding season lasts from November until April-May. When the eggs are laid they measure 0·78 by 0·60 mm., and at hatching they measure from 1·20 to 1·30 mm. Hatching takes place during March-April. Liberated larvae measure from 2·40 to 3·40 mm.

6. The number of eggs laid increases with size. The smallest number of eggs found was 136 and the largest 3,796. Shrimps of carapace lengths between 8·0 and 10·0 mm. lay between 200 and 600 eggs; shrimps between 11·0 and 13·0 mm. lay 600 to 1,300 eggs, while those between 14·0 and 17·0 mm. carry from 1,500 to 3,000.

7. *Pandalus montagui* exhibits sex reversal, but the population also includes a considerable number of primary females. After a period of 13 to 16 months the males show female characteristics. The male gonads sectioned showed developing oocytes. The causes of these sudden changes are not well understood.

8. Growth in *Pandalus montagui* is rapid during the first year, but becomes slight during the next two or three years. The male 0-group attains a mean carapace length of $\pm$ 10.0 mm. by November, and the female 0-group $\pm$ 11.00 mm. Growth stops during the winter months. *P. montagui* live three to four years; age cannot be judged from size alone.

9. The food of *Pandalus montagui* consists mainly of polychaetes, 66 to 84%, of which 30 to 52% is definitely 'ross' (*Sabellaria spinulosa*). Pink shrimps, however, feed also on crustaceans, small lamellibranchs, hydroids and algae. Some inactivity in feeding was noticed before the period of egg laying. Variations in the composition of stomach contents were observed in specimens obtained from different grounds.

10. *Pandalus montagui* is gregarious and migratory. Pink shrimps in the Thames Estuary migrate to deeper water in the late autumn and return by the middle or end of April. These movements may be correlated with salinity and temperature. One of the wintering grounds has been located off the Suffolk coast at depths of 30-40 m. In the Wash, where it is assumed different hydrographical conditions prevail, pink shrimps remain longer over the grounds. Pink shrimps also exhibit summer migrations. These are due either to search for food, or to movement away from very high temperatures during the summer months.

11. The bopyrid isopod *Hemiarthrus abdominalis* was the only parasite found on *Pandalus montagui*. The percentage infection was small, usually less than 3%, for the Thames Estuary populations, but may vary over a period of years. Parasitization of males causes an early suppression of the secondary male characteristics and a precocious sex change.

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APPENDICES

Appendix I

List of Invertebrata except Mollusca, with their frequencies, observed in 130 trawl and dredge hauls made during a period of 32 months, May 1950 to December 1952

Species	*Frequency*	*Numbers*				
		Occasional 1–10	*Common* 11–20	*Abundant* 21–50	*V. abundant* 51–100	*V.V. abundant* > 100
Carcinus maenas	67	16	16	18	14	3
Portunus sp.	63	15	10	22	12	4
Asterias rubens	50	25	13	8	2	2
Sabellaria spinulosa	47	6(1)*	18(8)	10(2)	1(1)	–
Sertularia argentea	44	13	19	9	3	–
Eupagurus bernhardus	32	26	5	1	–	–
Flustra foliacea	24	6	11	6	1	–
Porcellana longicornis	23	10	5	7	1	–
Hyas araneus	21	17	3	1	–	–
Alcyonidium gelatinosum	20	8	5	5	2	–
Macropodia rostrata	17	15	2	–	–	–
Halecium sp.	16	10	5	1	–	–
Solaster papposus	16	12	4	–	–	–
Pleurobrachia pileus	14	6	2	–	1	5
Hydrallmania falcata	13	10	3	–	–	–
Leander squilla	13	12	1	–	–	–
Praunus flexuosus	12	8	1	2	1	–
Homarus vulgaris	10	10	–	–	–	–
Aurelia aurita	9	5	4	–	–	–
Lepidonotus squamatus	9	9	–	–	–	–
Sabella pavonina	8	1	2	2	3	–
Ophiura albida	8	6	2	1	–	–
Spirontocaris cranchi	8	8	–	–	–	–
Pandalina brevirostris	7	7	–	–	–	–
Sacculina carcini	6	–	2	3	1	–
Corophium sp.	6	4	2	–	–	–
Vesicularia spinosa	6	4	2	–	–	–
Psammechinus miliaris	6	5	1	–	–	–
Nereis sp.	6	6	–	–	–	–
Nephthys sp.	6	6	–	–	–	–
Portunus arcuatus	5	5	–	–	–	–
Aeolidia papillosa	5	5	–	–	–	–
Schistomysis kervillei	5	5	–	–	–	–
Dendrodoa grossularia	4	2	1	1	–	–
Molgulla manhattensis	4	1	3	–	–	–
Harmothoë sp.	4	4	–	–	–	–
Idotea linearis	4	4	–	–	–	–
Hippolyte varians	4	4	–	–	–	–
Ophiura texturata	3	1	2	–	–	–
Diadumene cincta	3	2	1	–	–	–
Portunus puber	3	2	1	–	–	–
Ophiothrix fragilis	3	3	–	–	–	–
Sphaeroma serratum	3	3	–	–	–	–
Processa canaliculata	3	3	–	–	–	–
Bopyrus squillarum	3	3	–	–	–	–
Halichondria panicea	2	1	–	1	–	–
Aphrodite aculeata	2	2	–	–	–	–
Glycera sp.	2	2	–	–	–	–
Gammarus locusta	2	2	–	–	–	–
Siriella armata	2	2	–	–	–	–
Crangon allmanni	2	2	–	–	–	–
Hyas coarctatus	2	2	–	–	–	–
Haliclona oculata	1	1	–	–	–	–
Tubularia sp.	1	1	–	–	–	–
Nemertesia antennina	1	1	–	–	–	–
Sertularia gracilis	1	1	–	–	–	–
Alcyonium digitatum	1	1	–	–	–	–
Sagartia elegans	1	1	–	–	–	–
Metridium senile	1	1	–	–	–	–
Amphicteis gunneri	1	1	–	–	–	–
Pomatoceros triqueter	1	1	–	–	–	–

*Figures in parenthesis denote dead colonies.

Appendix I—*continued*

Species	*Frequency*	*Numbers*				
		Occasional 1–10	*Common* 11–20	*Abundant* 21–50	*V. abundant* 51–100	*V.V. abundant* > 100
Phascolosoma vulgare	1	1	–	–	–	–
Dexamine spinosa	1	1	–	–	–	–
Gastrosaccus spinifer	1	1	–	–	–	–
Mesopodopsis slabberi	1	1	–	–	–	–
Spirontocaris pusiola	1	1	–	–	–	–
Portunus pusillus	1	1	–	–	–	–
Portunus depurator	1	1	–	–	–	–
Cancer pagurus	1	1	–	–	–	–
Pinnotheres pisum	1	1	–	–	–	–
Ebalia tuberosa	1	1	–	–	–	–
Pilummus hirtellus	1	1	–	–	–	–
Scrupocellaria scruposa	1	1	–	–	–	–
Ascidiella aspersa	1	1	–	–	–	–

Appendix II

List of Mollusca and Algae, with their frequencies, observed in 130 *trawl and dredge hauls made during a period of* 32 *months, May* 1950 *to December* 1952

Species	*Frequency*		*Numbers*									
			Occasional 1–10		*Common* 11–20		*Abundant* 21–50		*V. abundant* 51–100		*V.V. abundant* > 100	
	Live	*Shell*	*Live*	*Shell*	*Live*	*Shell*	*Live*	*Shell*	*Live*	*Shell*	*Live*	*Shell*
Mytilus edulis	26	15	10	1	4	7	5	7	3	–	4	–
Buccinum undatum	21	21	14	5	7	6	–	1	–	–	–	–
Crepidula fornicata	20	1	20	–	–	–	–	1	–	–	–	–
Nucula nucleus	11	6	5	–	4	3	1	2	1	1	–	–
Sepiola atlantica	10		6		3		1		–		–	
Abra alba	8	8	5	1	2	4	1	3	–	–	–	–
Gibbula cineraria	4	6	4	3	–	1	–	2	–	–	–	–
Modiolus modiolus	4	2	4	1	–	1	–	–	–	–	–	–
Musculus discor var. *angustior*	4	–	3	–	–	–	–	–	–	–	1	–
Sepia officinalis	4		4		–		–		–		–	
Ostrea edulis	3	26	3	4	–	12	–	10	–	–	–	–
Lora rufa	3	–	3	–	–	–	–	–	–	–	–	–
Macoma balthica	2	6	2	–	–	5	–	1	–	–	–	–
Spisula elliptica	2	4	2	–	–	2	–	2	–	–	–	–
Cardium exiguum	2	3	2	1	–	2	–	–	–	–	–	–
Nassarius reticulatus	2	2	1	1	1	1	–	–	–	–	–	–
Spisula solida	2	2	2	2	–	–	–	–	–	–	–	–
Mya arenaria	2	2	2	2	–	–	–	–	–	–	–	–
Hiatella arctica	2	2	2	2	–	–	–	–	–	–	–	–
Lacuna crassior	2	–	1	–	–	–	1	–	–	–	–	–
Nucella lapillus	1	5	1	3	–	2	–	1	–	–	–	–
Petricola pholadiformis	1	4	1	–	–	3	–	–	–	–	–	–
Urosalpinx cinerea	1	3	1	3	–	–	–	–	–	–	–	–
Scrobicularia plana	1	1	1	1	–	–	–	–	–	–	–	–
Neptunea antiqua	1	1	1	1	–	–	–	–	–	–	–	–
Alloteuthis media	1		–		1		–		–		–	
Abra nitida	1	–	1	–	–	–	–	–	–	–	–	–
Venerupis rhomboides	1	–	1	–	–	–	–	–	–	–	–	–
Beringius turtoni	1	–	1	–	–	–	–	–	–	–	–	–
Cardium edule	–	17	–	5	–	9	–	3	–	–	–	–
Ocenebra erinacea	–	11	–	9	–	2	–	–	–	–	–	–
Chlamys varia	–	8	–	4	–	3	–	1	–	–	–	–
Chlamys opercularis	–	3	–	1	–	1	–	1	–	–	–	–
Venerupis aurea	–	2	–	2	–	–	–	–	–	–	–	–
Abra prismatica	–	1	–	1	–	–	–	–	–	–	–	–
Mya truncata	–	1	–	1	–	–	–	–	–	–	–	–
Dentalium entalis	–	1	–	1	–	–	–	–	–	–	–	–
Lepidochitona cinereus	2		2		–		–		–		–	
Ulva sp.	12		1		8		1		2		–	
Laminaria sp.	3		1		2		–		–		–	

Appendix III

List of fish, with their frequencies, observed in 130 trawl hauls made during a period of 32 months, 4 May 1950 to 22 December 1952

Species	Frequency	Numbers				
		Occasional 1–10	*Common* 11–20	*Abundant* 21–50	*V. abundant* 51–100	*V.V. abundant* > 100
Agonus cataphractus	88	36	29	19	4	–
Gobius minutus	80	21	14	27	17	1
Gadus merlangus	73	29	16	17	10	1(126)
Limanda limanda	69	43	15	67	4	–
Gadus luscus	65	37	10	12	2	4(135–280)
Raja clavata	51	46	5	–	–	–
Liparis vulgaris	46	19	16	9	–	2
Solea lutea	46	28	7	9	2	–
Onos mustela	42	40	1	1	–	–
Clupea sprattus	39	24	10	3	2	–
Cottus scorpius	37	33	2	1	1	–
Gobius niger	35	24	7	2	2	–
Pleuronectes platessa	35	32	3	–	–	–
Callionymus lyra	30	27	2	1	–	–
Solea vulgaris	26	22	4	–	–	–
Syngnathus acus	19	17	2	–	–	–
Centronotus gunnellus	17	16	1	–	–	–
Clupea harengus	14	8	4	2	–	–
Pleuronectes microcephalus	12	9	3	–	–	–
Gadus minutus	8	4	3	1	–	–
Scyllium canicula	6	6	–	–	–	–
Morone labrax	6	6	–	–	–	–
Pleuronectes flesus	5	5	–	–	–	–
Anguilla vulgaris	4	4	–	–	–	–
Zoarces viviparus	3	3	–	–	–	–
Trigla hirundo	3	3	–	–	–	–
Gasterosteus aculeatus	2	2	–	–	–	–
Ammodytes lanceolatus	2	2	–	–	–	–
Cottus bubalis	1	1	–	–	–	–
Ammodytes tobianus	1	1	–	–	–	–
Petromyzon fluviatilis	1	1	–	–	–	–
Gadus callarias	1	1	–	–	–	–
Gadus pollachius	1	1	–	–	–	–
Trigla gurnardus	1	1	–	–	–	–
Mullus surmuletus	1	1	–	–	–	–
Rhombus laevis	1	1	–	–	–	–

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